Movement Patterns of Field Rodents in Hawaii[1]

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ABSTRACT: The setting for a 10-year study of the ecology of the plague organism is described. Four rodents, *Mus musculus, Rattus exulans, R. rattus* and *R. norvegicus,* were investigated during 1959–64 by the mark-and-release method, with numerous grids and lines of traps set in coastal fields of sugar cane and in adjacent uncultivated lands, primarily rugged gulches. Fluctuations in population densities are related to season, to cultural practices for sugar cane, and to the movement and home range of rodents. Harvest of the cane is a catastrophe for rodent populations in the fields, and few that escape to adjacent lands survive to become established there. Patterns of movement are remarkably similar in the four species, but gradients toward longer movements follow trends for greater body size. Significant differences in distances moved are derived between species and between sexes within species, in time and in different habitats. Home range and local movement of the field rodents of Hawaii have many parallels with those of the same species as reported in other regions of the world and in other cultural surroundings, but direct comparisons are seldom possible because of differences in methods used and in environmental conditions.

THIS STUDY of movement patterns in rodents is part of a long-term biomedical program that extended from 1958 to 1968 in the Hamakua District, on Hawaii, the largest and southernmost island of the Hawaiian chain. A principal aim of this program was to study the ecology of small mammals, their fleas, and the plague bacillus, in order to improve methods of plague suppression (see Quan et al., 1965; Meyer et al., 1965; Haas, 1965, 1969; Haas, Wilson, and Tomich, 1969). Because plague-infected rodents and fleas have been found repeatedly in Hamakua sugar cane fields, our work was concentrated in that habitat. The information presented in this report can therefore be applied not only to rural plague control, but also to other public health problems involving rats, and to eradication of rats that damage sugar cane and other agricultural crops. Rodents have commanded the attention of several previous projects designed to alleviate economic loss and danger to human health in specific regions of Hawaii. These studies were reported principally by Pemberton (1925), Eskey (1934), Dopmeyer (1936), Spencer (1938), Doty (1945), and Kartman and Lonergan (1955*a*).

The Hawaiian rodent fauna comprises four species, the native *Rattus exulans,* presumably brought by man from the South Pacific during early settlement of the islands, and *Mus musculus, Rattus norvegicus* and *Rattus rattus,* all cosmopolitan forms that arrived only in modern times after European discovery of the islands (Tomich, 1969). *Rattus rattus* is represented by three phenotypes for coat color that are sometimes erroneously referred to as distinct subspecies (Tomich and Kami, 1966; Tomich, 1968*a*).

MATERIALS AND METHODS

Regional Description

The study region is on the lower northeastern slope of Mauna Kea, a dormant volcanic mass whose summit rises 13,796 ft above sea level. The land slopes steeply at 500 to 600 ft per mile and ends in cliffs usually 50 to 150 ft high, overlooking rubbled, surf-swept beaches of the Pacific Ocean. At the northwest end of the region, these cliffs at Waipio Bay are as high as

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800 ft, and merge with precipitous slopes raised as much as 1,500 ft above Waipio Valley. Throughout the Hamakua District ancient erosion gulches, that are characteristically deep and often with nearly vertical sides, occur at intervals averaging 0.5 mile. These gulches form boulder-strewn drainage channels for flood waters which result from occasional torrential rains. Springs and live streams are few. Sugar cane is the principal agricultural crop, and it occupies a belt some 3 miles wide, from the cliff's edge to about 2,000 ft above the sea. Remnant tracts of native forest, planted forest, and pasture lands extend to higher elevations. Kartman and Lonergan (1955*b*, pp. 58–60) figure typical gulch and cane-field vegetation.

Climate of the Hamakua District is weakly tropical. Even though the day length ranges from 11.5 to 14 hours, seasonal changes are slight because of the tempering effect of marine conditions that produce seasonal winds and daily cloud formations. Average annual temperature at sea level is about 72°F along the Hamakua Coast and the mean range is approximately 6°F. Temperature drops at the approximate rate of 3°F per thousand feet in a transect from sea level to the summit of Mauna Kea. Mean rainfall at Paauhau Mill (elevation 400 ft) is 66 inches per year, and at the head of the Lower Hamakua Ditch near Kukuihaele (elevation 980 ft) it is 79 inches. Rain falls the year around but is concentrated in the winter months, averaging at Honokaa Town (elevation 1,100 ft and 89 inches total) 9.2 inches per month from October through April, and 4.9 inches per month from May through September (Blumenstock and Price, 1967).

Food supplies for rodents are continuous. Besides fruits, seeds, and other plant materials in waste areas, weeds (principally grasses, legumes, and composites) are usually abundant in the cane fields. Rats commonly eat cane internodes and grass stalks; the house mouse lives more strictly on seeds and insects (Kami, 1966). Rodents nest underground, in stone piles, in rocky out-crops, or under the roots of trees and sugar cane. Within our study areas *Rattus rattus* does not nest in trees, nor does *Mus musculus* nest in dense grass or in leaf litter at the ground surface.

The Field Program

Field information was gathered by the marking and release of rodents captured in cage-style traps. These traps were set in grid patterns within cane fields and in adjacent gulches, following primarily the methods of Davis (1956), or in lines along or within the gulches. The trap grids were designed to determine local movement and movement between grids. The lines of traps served to intercept marked rodents near or at a distance from the grids, and to provide marked animals which sometimes moved into the grids. Another program, in which snap traps were used (to be reported on elsewhere), also assisted in recovery of marked rodents at variable distances from the cage-trap grids and lines.

Choice of study areas was governed in part by previous occurrences of plague. One location was near the Paauhau Sugar Company mill (Fig. 1) including Field 001, its adjacent gulches, and neighboring cane fields and gulches. Field 001 was ditch-irrigated, and thus periodically saturated. This 108-acre field was planted solidly to sugar cane in contour rows, except for an access road diagonally crossing it, and for three rock piles (since removed) totaling less than one acre. The lower edge of the field is bounded by ironwood trees (*Casuarina equisetifolia*) in single rows or in narrow groves along the cliff. Planted cane begins 120 ft above sea level and extends to 480 ft at the top of the field. Between Field 001 and the Paauhau Mill to the east is Kahaupu Gulch, one of the largest in the region. It is 300 to 500 ft wide and in several places nearly 150 ft deep. Along each rim of this gulch is an almost continuous band of ironwood trees. The gulch walls are well-clothed with vegetation; in addition to ironwood, kukui (*Aleurites malaccensis*), Java plum (*Eugenia cumini*), and lemon guava (*Psidium guajava*), there is a variable understory of lantana (*Lantana camara*), purple panic grass (*Panicum purpurascens*), palm grass (*Setaria palmifolia*), and other exotics whose distribution and abundance depend in part on conditions of exposure and moisture. A few insignificant native species are present.

At the west edge of Field 001 is Ku-

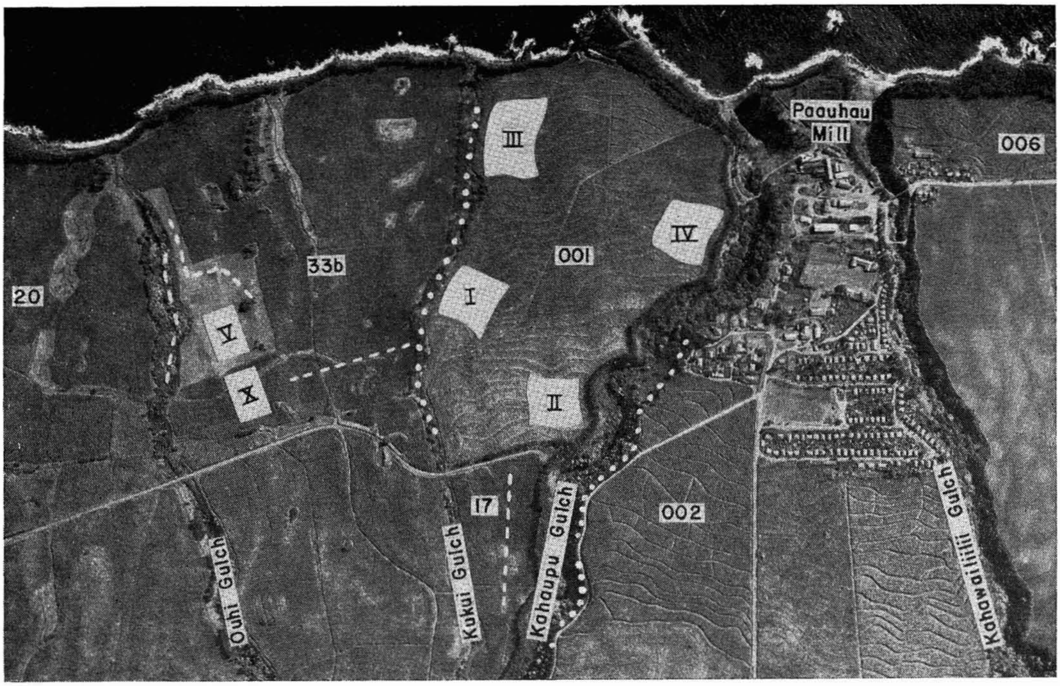

FIG. 1. Aerial view of Paauhau study area. Overlays show arrangement of rodent trapping grids and lines, and prominent physical features. Inscription as in Figure 2. (Photo by R. M. Towill Corporation, Honolulu.)

kuiaonanipahu Gulch (referred to subsequently in this paper as Kukui Gulch), a shallow bedrock channel 5 to 30 ft deep and with its sides generally covered by purple panic grass and Guinea grass (*Panicum maximum*). Ironwood, Java plum, kukui, and lemon guava are the principal trees scattered along this gulch. Field 001 is bounded at the upper side by a narrow strip of stone piles, trees, shrubs and grasses, and a plantation road. Fields 17 (above 001) and 33b (across Kukui Gulch), both in the Honokaa Sugar Company plantation, were unirrigated at the time the major part of this study was in progress.

Four grids (I–IV) were placed in Field 001. Each consisted of 54 traps in six rows of nine traps each, along contour irrigation ditches. Individual traps were spaced at 50 ft in the rows, but spacing between rows was governed by the winding contour ditches which varied from 35 to 250 ft apart. A roadside check line was laid along the far rim of Kahaupu Gulch, and a similar one was placed in the shallow bed of Kukui Gulch.

Live-trapping continued for 20 months in Field 001, through one crop cycle, from December 1959 when the cane was two months old, until July 1961 when harvest began. Snap-trap lines, each with 20 stations of three traps each, the stations spaced at 50-ft intervals, were established in Fields 006, 17, 33b, and in Spencer Field (cleaver-shaped grassy area, Fig. 1), in Ouhi Gulch adjacent to the grassland, and in Field 20, ½ mile west of Ouhi Gulch.

Spencer Field was a second center of mark-and-release effort. Sugar cane cultivation was terminated in this 12-acre area in 1948. The land thereafter lay as an undisturbed wasteland and had gradually produced a stable covering, almost exclusively of Guinea grass, but remnant patches of cane remained. A small thicket of guava, scattered bushes of haole koa (*Leucaena glauca*), and two clumps of Java plum trees, were essentially the only woody plants. Several stone piles were scattered in the field and provided some harborage for rodents. Grid V, in Spencer Field, was operated for 60 months, beginning in October 1959. Adjacent, in Field

33b, Grid X was established late in the program; it ran for 28 months, beginning in March 1962, and was terminated concurrently with Grid V. Sugar cane in this 97-acre field was much retarded by drought until sprinkler irrigation began in March 1963; hence the unusually long crop cycle of more than 28 months. Grids in Spencer Field and in Field 33b were each of 54 traps spaced at 50-ft intervals in six rows of nine traps each.

The third trap complex was 8 miles away to the northwest, near Kukuihaele Village, chiefly in Field 101b and in a wooded gulch within that field. Field 101b (Fig. 2) consists of 38 acres of unirrigated cane on a cliff from 700 to 1,000 ft above Waipio Bay and the mouth of Waipio Valley. This small field is interrupted by rocky waste areas, shallow gulches, and a county road. Its upper boundary (at 980 ft elevation) is the Lower Hamakua Ditch, a concrete flume that receives water near the northwest corner of the field via a 7-mile tunnel from the Kohala Mountain watershed. Field 111 lies above the ditch, and Kukuihaele Village borders Field 101b on the east. The county road crosses the field at the head of a short, hanging valley referred to in this paper as 101b Gulch. This area is planted in ironwood. Its moderately steep sides contain several massive rock outcrops, but the bottom has an intact soil mantle, for there is no watercourse. Toward the lower end, kukui is the principal tree. There is an understory of guava, ti (*Cordyline terminalis*), palm grass, and honohono (*Commelina nudiflora*). Vegetation extending over the lip of the precipice at the mouth of 101b Gulch and the lower border of Field 101b is principally kukui, screw pine (*Pandanus tectorius*), ti, and panic grasses. The cliff face gradually steepens and becomes a rough rock wall several hundred feet high, bare or only sparsely vegetated.

Two trap grids (VI and VII) in 101b Gulch were each of six rows of nine traps spaced at 35-ft $\times$ 50-ft intervals because of the restricted gulch area; two similar grids (VIII and IX) in the open sugar cane field of Field 101b had traps spaced the normal 50 ft each way. Grids VI and VII were run continuously for 48 months between July 1959 and June 1963. Grids VIII and IX in the field were laid out in

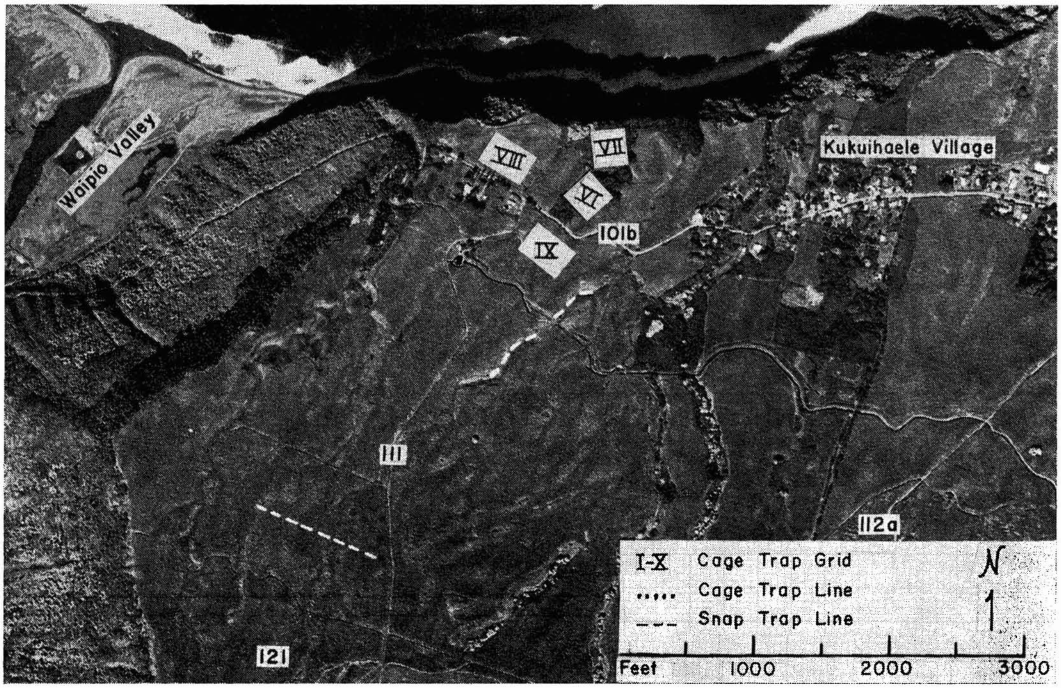

FIG. 2. Aerial view of Kukuihaele study area. Overlays show arrangement of rodent trapping grids and lines, and prominent physical features. (Photo by R. M. Towill Corporation, Honolulu.)

2-month old cane, as were the grids of Field 001 and Field 33b. The 101b grids were operated for 21 months, from July 1959 through March 1961, when the crop was harvested. Grid VIII was run again in the following crop cycle for another purpose and was useful in tracing movement of some rodents marked during that time in 101b Gulch. Standard snap-trap lines were laid in a small gulch adjacent to Grid IX, in Field 111, and in four fields south of Field 111.

All check lines and grids were run each month the year around. They were baited and set on Monday and closed on Friday of the week or weeks used. Check lines were usually run for 2 weeks per month, and a program of trapping out, for as long as 30 days, terminated use of selected lines or grids. Squares of fresh coconut were the standard bait. Brief trials were made with ripe banana, but coconut was superior because of better keeping qualities.

Captured rodents were examined in the field under ether anesthesia. Body weight, sex, and an assessment of reproductive status and age were recorded. Fleas were removed for use in other phases of the overall program. Rats and mice were marked with #1 fingerling fish tags clipped to the ear. Although some tags were lost, it was not practical to superimpose a toe-mark system on the ear-tag method. A daily chronological field record was kept and these data were transferred to permanent summary files.

Mean values of distances moved were compared by Wilcoxon's rank test (Steel and Torrie, 1960, pp. 405, 434), a test designed for arrays of nonparametric data. Calculations were performed by an IBM 360/20 computer programmed in the RPG system. Population estimates were obtained by the modified Lincoln index method devised by Hayne (1949).

Four consecutive years of subnormal rainfall favored field operations, but a destructive flood occurred early in April 1961 when 22 inches of rain fell in less than a day at Paauhau. No trap line was in use at that time, but 39 of 54 cage traps in Kukui Gulch were flushed into the sea in spite of the precaution of hanging them on trees or placing them high on the gulch bank when closed some days earlier.

RESULTS

Population Levels

Annual fluctuations in density are characteristic of the Hamakua rodent populations. In the undisturbed 101b Gulch habitat these rhythmic changes in abundance are clearly demonstrated over a 4-year period (Fig. 3). In general, a slight early-summer increase of rodents is followed by a great early-winter increase and a drastic late-winter decrease. This conclusion is substantiated by a concurrent study of snap-trapped rodents, from which annual cycles of pregnancy rates and age classes were obtained (Tomich, unpublished data).

Seasonal variation in response to traps was of little apparent significance. In the mouse, amplitudes of densities are generally greater than those in rats, and greater in *R. exulans* than in *R. rattus*. *R. norvegicus* was declining rapidly, and totally disappeared from the countryside during the study period; hence, rather few data are available for this species. Drought conditions in 1961–63 were accompanied by variously reduced rodent populations in 101b Gulch. Mice deserted the area completely for many months, but they were still common in the adjacent cane field.

In Spencer Field, a second undisturbed habitat, populations were generally sparse, were subject to considerable mortality from closely adjacent snap traps, and were difficult to estimate because of low trap yield (Fig. 4).

Growth and harvest of sugar cane, in its usual crop cycle of about 22 months, modifies conditions of food and cover for rodents on cane lands and enforces rigid controls on their normal annual cycles of increase and decrease. Early summer harvest appears to permit the normal increase of rodent numbers; late summer harvest seems to curtail it and to result in failure, at least of *R. exulans*, to attain high densities before the end of the next crop cycle. Field 001 (Fig. 5) was harvested in September 1959, and trapping began in December when the cane was about 3 feet tall. Both *M. musculus* and *R. exulans* established themselves only slowly in the field, and the fall reproductive period resulted in no sizable population of either species. *M. musculus*, however, responded in the summer of 1960 with a high

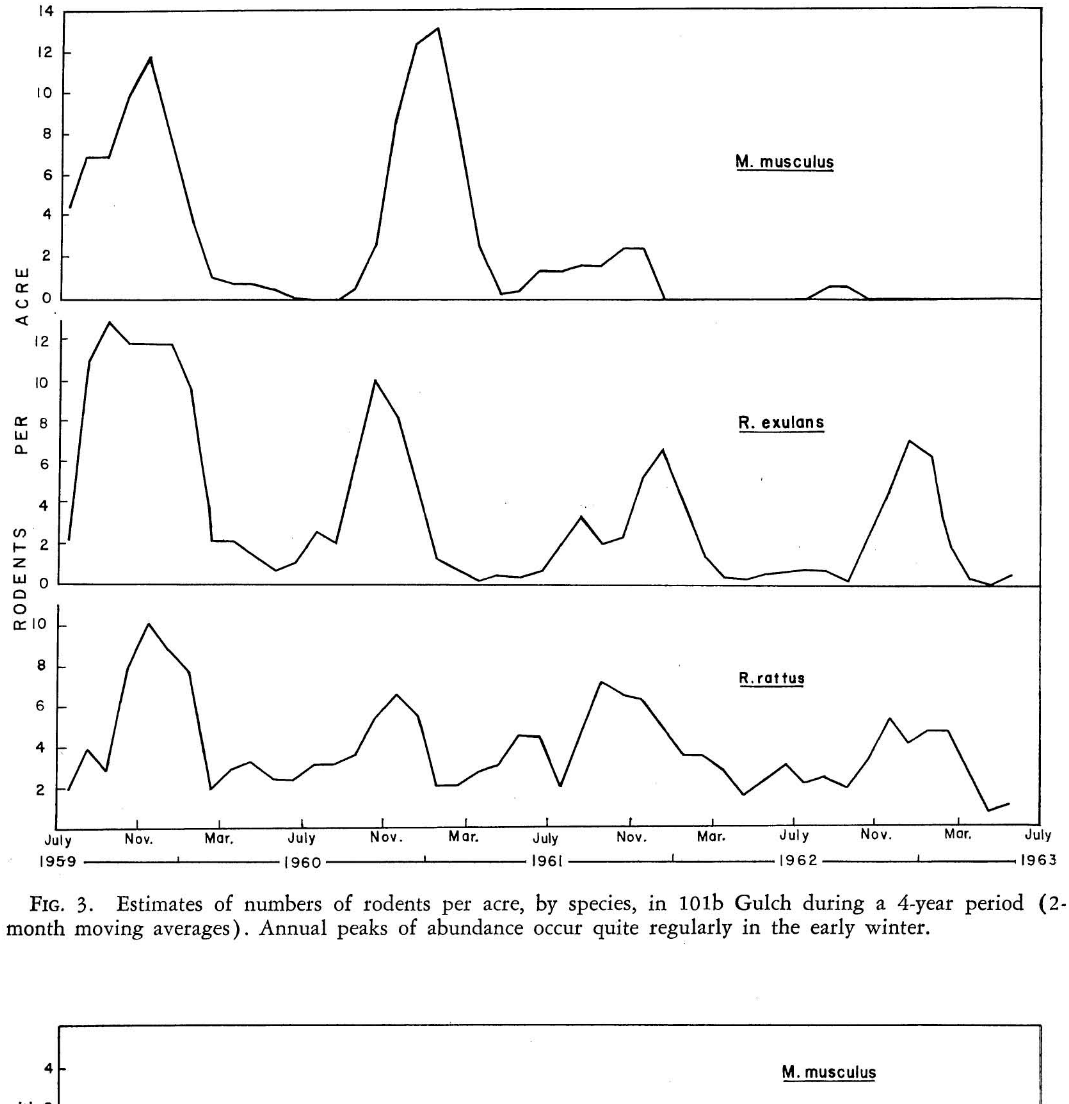

FIG. 3. Estimates of numbers of rodents per acre, by species, in 101b Gulch during a 4-year period (2-month moving averages). Annual peaks of abundance occur quite regularly in the early winter.

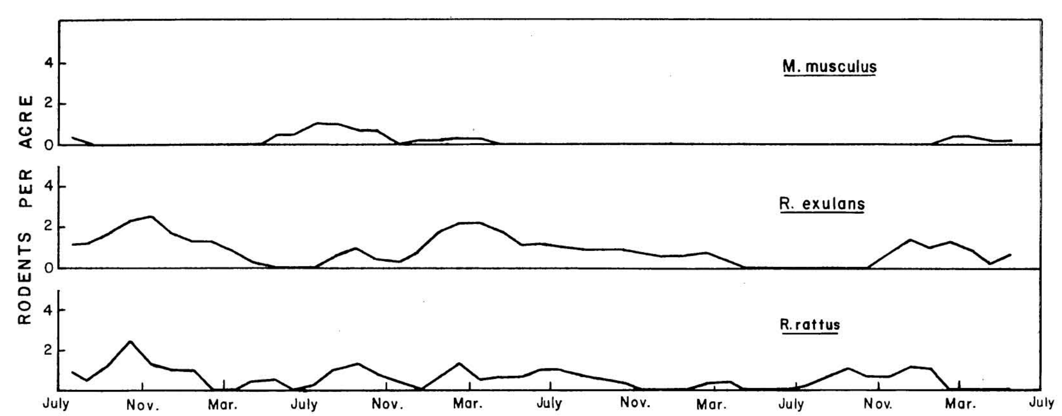

FIG. 4. Estimates of numbers of rodents per acre, by species, in Spencer Field during a 4-year period (2-month moving averages). The population was sparse and shows irregular periods of abundance and absence.

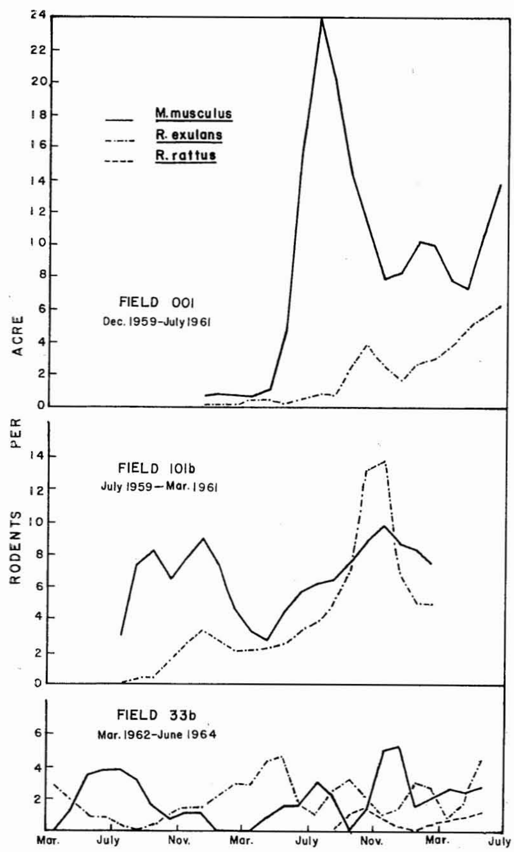

FIG. 5. Estimates of numbers of rodents per acre, by species, during a crop cycle in each of three Hamakua District sugar cane fields (2-month moving averages). Rise in population levels is controlled, in part, by season of previous cane harvest.

population peak such as occurs sporadically in the Islands. The greatest populations of Hawaii Island arise in dry grassland or in open forest rather than in sugar cane fields (Tomich, 1969). Mice in Field 001 retained the high-density pattern by dropping to moderate numbers in the winter; then they began another steep summer increase, which was halted by harvest of the field in August 1961. *R. exulans* attained a slight peak in population only by early winter of 1960 when the cane was about 14 months old; then numbers declined and only gradually increased in the following summer until harvest of the field.

In contrast, Field 101b was harvested in April 1959 and trapping began in July when the new cane again was about 3 feet tall (Fig. 5). *M. musculus* quickly established itself in the field and normal cycles of abundance ensued. *R. exulans* was slow to populate the field, reproduced slowly in the first winter, and reached moderate abundance only in the second winter. Harvest of the cane crop in April 1961 terminated the study when both species were in a late-winter decline.

Field 33b (Fig. 5) was studied about 2 years later than the preceding fields, from March 1962 to June 1964. This field was severely affected by drought but became lush after initiation of sprinkler irrigation in March 1963. Rodent populations were generally out of phase, by species, and were generally small in size. *R. rattus,* unexpectedly, became relatively numerous late in the crop cycle. Because of these irregularities, population fluctuations in Field 33b cannot be considered typical.

Species composition of the 5,650 individual rodents trapped on all the study plots (Fig. 6) shows the following percentages: *M. musculus* 51.1, *R. exulans* 33.0, *R. rattus* 13.5, and *R. norvegicus* 2.4. *M. musculus* was most abundant in cane fields; *R. exulans* was common in all habitats; *R. rattus* occupied the gulches and grassland almost exclusively; and the few *R. norvegicus* present lived in all habitats.

This brief treatment of fluctuations in population levels of rodents during the study, and some of the factors controlling them, will serve as a reference for results of movement pattern investigations.

Day-to-day local movements of all rodents are a subject of special consideration, for they serve as indices of how much ground is required to furnish nutritional and behavioral needs within a brief period of time. Short-term exploitation of the environment, for a few weeks rather than for several months, is often the entire contribution of an individual rodent to progress of the population, because the life span is usually brief.

Mus musculus

The house mouse lived mainly in the cane fields but was also usually common in the gulches. Because data on this species are most numerous, it is considered first.

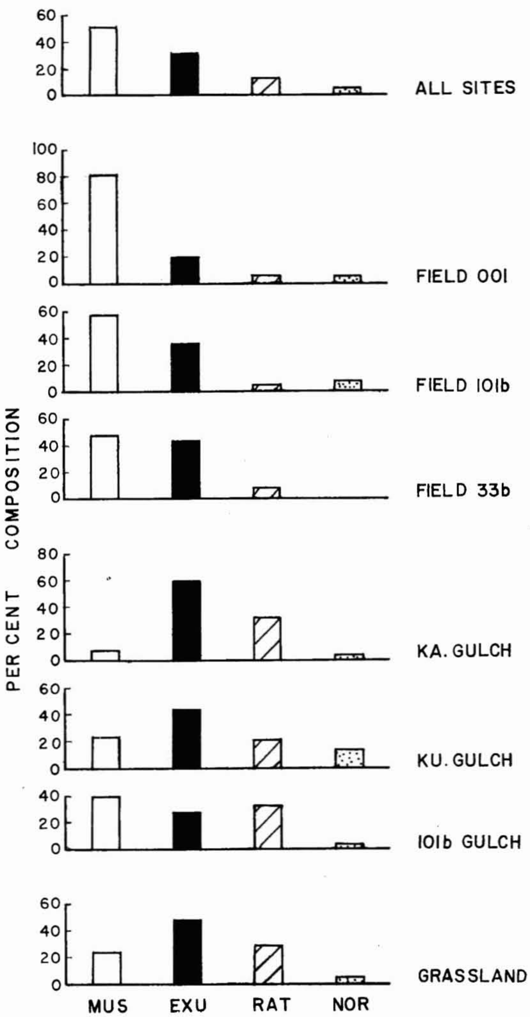

FIG. 6. Percentage composition, by species, of Hamakua rodent populations. Relative abundance and preference for three habitats are shown for the four Hawaiian field rodents.

LOCAL MOVEMENT: Brant (1962) has erected the measure, average distance between captures (av. D), to summarize movements of a rodent over a short or prolonged period of time. I have applied this unit of measure to recaptures within the 4-day trapping period (repeats), and to those separated by one or more months (returns). In summary, av. D for repeating males of *M. musculus* was 81 ft, and for females 69 ft. For returning males av. D was 91 ft, and for females, 75 ft (Table 1). Av. D for mice is remarkably uniform in the several habitats in spite of variations in terrain, vegetation, and trap arrangement. Obvious exceptions are for returns in Spencer Field—142 ft for males and 116 ft for females.

Emphasis in testing data of Table 1 was placed not on vertical comparisons between habitats, but on horizontal comparisons, as indicated. These tests (from P values) show different trends at the individual site, and in summary of the 2,663 examples of av. D, it is significantly greater in male than in female repeats (*ab*), significantly greater in returning males than in repeating males (*ac*), and highly significantly greater in returning males than in returning females (*cd*). Av. D for females in the two time classes (*bd*) was not statistically different.

According to Brant's (1962) method, when a rodent is captured in the trap of previous capture it registers a zero value for distance moved ($D = 0$). These values are included in the calculations along with the larger ones, and are valid expressions of the tendency of a rodent to remain in the area about a single trap or set of traps. A mouse returns about once in 4 times caught to the trap of its previous capture (Table 1). In another sense, in 3 out of 4 times caught the mouse enters a trap different from that of the earlier capture. There seems to be no difference in this behavior if the animal is caught repeatedly within one week, or at intervals of a month or more, but females, overall, have a slightly stronger tendency than males to enter the same trap on successive captures. In Field 001 and in all gulches, results are quite similar. On the other hand, Field 101b mice were less frequently trapped successively in the same trap, only about once in 8 times for males and once in 5 times for females; for Spencer Field and for Field 33b the pattern is somewhat erratic.

Av. D tends to increase with time elapsed between recaptures, markedly in males, and slightly in females (Table 2). This may reflect a more frequent change of residence by males and possibly a more extensive use of the home range by them. Nearly 80 percent of all mice recaptured were caught in the month following a previous capture, and nearly 95 percent were retaken within 2 months. Thus, among the mice prone to recapture once they have been

TABLE 1

AVERAGE DISTANCE IN FEET BETWEEN CAPTURES (av. D) AND RATE BY PERCENTAGE OF RECAPTURE IN TRAP OF PREVIOUS CAPTURE (% D = 0), FOR *Mus musculus*, AT TWO LEVELS OF ELAPSED TIME AND UNDER VARIOUS ARRANGEMENTS OF TRAPS, BY SEX, AND IN VARIOUS HABITATS

	REPEAT WITHIN 4-DAY TRAPPING PERIOD (R)						RETURN AFTER ONE OR MORE MONTHS (R1)						P VALUES FROM RANK TEST OF av. D			
	Males (a)			Females (b)			Males (c)			Females (d)						
SITE	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0	(ab)	(cd)	(ac)	(bd)
Field 001 50 × 50+-ft grids	78	(481)	26.1	63	(325)	29.3	86	(498)	25.7	75	(424)	27.8	.015*	.007**	.046*	.109
Field 101b 50 × 50-ft grids	92	(174)	10.3	76	(111)	14.4	97	(135)	13.3	66	(100)	25.0	.136	.002**	.337	.046*
101b Gulch 35 × 50-ft grids; 50-ft gulch lines	78	(53)	28.3	62	(52)	28.8	91	(66)	25.8	64	(53)	35.8	.436	.034*	.068	.221
Spencer Field and Field 33b 50 × 50-ft grids	88	(68)	26.5	93	(47)	18.4	142	(40)	14.7	116	(36)	24.1	.245	.138	.007**	.326
Summary	81	(776)	22.8	69	(535)	25.3	91	(739)	22.9	75	(613)	27.9	.017*	.000**	.011*	.468

* Significant ($P < .05$).
** Highly significant ($P < .01$).

TABLE 2

AVERAGE DISTANCE IN FEET BETWEEN CAPTURES (av. D) AND PERCENT OF EXAMPLES IN EACH CLASS (%) FOR *Mus musculus*, BY TIME INTERVAL IN MONTHS SINCE PREVIOUS CAPTURE AND BY SEX, FOR THE SEVERAL STUDY PLOTS

	NUMBER OF MONTHS SINCE PREVIOUS CAPTURE											
	1			2			3			4 or more		
SITE	av.D	(n)	%	av.D	(n)	%	av.D	(n)	%	av.D	(n)	%
Field 001												
M	81	(415)	82.8	117	(67)	13.4	99	(15)	3.0	141	(4)	0.8
F	75	(335)	78.6	71	(69)	16.2	78	(15)	3.5	136	(7)	1.6
Field 101b												
M	91	(105)	77.8	132	(22)	6.3	44	(5)	3.7	158	(3)	2.2
F	67	(77)	77.8	43	(11)	11.1	74	(3)	3.0	85	(8)	8.1
All gulches												
M	84	(43)	66.2	122	(18)	27.7	50	(4)	6.2	–	(0)	–
F	66	(41)	78.8	40	(5)	9.6	74	(2)	3.8	103	(4)	7.7
Spencer Field and Field 33b												
M	119	(31)	81.6	162	(1)	2.6	265	(4)	10.5	211	(2)	5.3
F	136	(18)	50.0	91	(10)	27.8	150	(3)	8.3	75	(5)	13.9
Summary												
M	85	(594)	80.4	120	(108)	14.6	106	(28)	3.8	162	(9)	1.2
F	75	(471)	76.8	68	(95)	15.5	87	(23)	3.8	101	(24)	3.9

marked, there is a high probability of their capture during any 2-month period of their existence in the study plots.

When mice were scarce in young cane they tended to be more mobile than is usual, and this is evident in their av. D in each habitat, except in Field 33b (Table 3). The pattern was present in both sexes, and so the data are pooled. The summary figure of 118 ft for the first 4-month period ($n = 87$) is 55.3 percent larger than the 76 ft average for the succeeding four periods ($n = 1{,}908$). Yet, each of the three fields studied showed a different pattern. In Field 001, av. D was longest of all at 149 ft ($n = 30$) in the first growth period of the cane; it shortened drastically in the second period, then gradually increased above the average, only to drop again in the final period before harvest. In Field 101b there was a general decline in av. D throughout the cane cycle, while in Field 33b there was a gradual increase. Comparisons with estimated densities of mice in the fields (Fig. 5) and reference to the starting dates of the studies (December, July, and March, respectively) do not fully reveal the causes of these differences. It is probable, at least, that the perennial sparseness of mice in Field 33b promoted their increasing movement as the cane covered the field and reached maturity, a feature not observed in other populations. Rate of return to the trap of previous capture (% D = 0) is quite consistently inverse to the lengths of av. D, and hence, to population density.

HOME RANGE: The land that a rodent uses with some regularity during its lifetime can be expressed by linear as well as by areal measure. I have followed Stickel (1954) in her use of the linear measure, adjusted range length (ARL). Briefly, ARL is the straight-line distance between the most widely separated sites of capture for the individual rodent, with a correction factor of one-half the distance to the next nearest trap added to each end. A mouse, for example, caught in traps 147 ft apart had an ARL figure of 197 ft (147 + 25 + 25 ft) in a grid with 50-ft trap spacing.

In Field 001, because traps were placed at 50-ft intervals along the contour irrigation ditches, and because spacing of the ditches was variable, two classes of ARL measurement were possible: linear (L), along the ditches in multiples of 50 ft for rodents captured on only

TABLE 3

AVERAGE DISTANCE IN FEET BETWEEN CAPTURES (av. D) AND RATE BY PERCENTAGE OF RECAPTURE IN THE TRAP OF PREVIOUS CAPTURE (% D = 0), FOR *Mus musculus*, DURING FIVE 4-MONTH GROWTH PERIODS IN THE CROP CYCLES OF THREE SUGAR CANE FIELDS

	GROWTH PERIOD AND AGE OF CANE IN MONTHS														
	I 3–6			II 7–10			III 11–14			IV 15–18			V 19–22		
SITE	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0
Field 001	149	(30)	6.7	60	(91)	33.0	72	(608)	27.3	85	(391)	26.1	66	(354)	30.2
Field 101b	105	(46)	8.7	90	(76)	7.9	77	(45)	15.6	77	(146)	16.4	70	(138)	20.3
Field 33b	88	(11)	27.3	99	(30)	16.7	110	(8)	0	139	(7)	14.3	194	(14)	14.3
Summary	118	(87)	10.3	77	(197)	20.8	73	(661)	26.2	83	(544)	23.3	70	(506)	27.0

TABLE 4

TRAP SPACING AND GRID AREAS IN FIELD 001

GRID	MEAN SPACING OF TRAPS (IN FEET) L	NL	MAXIMUM DISTANCE BETWEEN TRAPS (IN FEET) L	NL	EFFECTIVE ACREAGE
I	50	75	450	590	6.6
II	50	74	450	540	7.1
III	50	123	450	735	10.5
IV	50	80	450	630	7.5

a single ditch, and nonlinear (NL) for those that ranged on two or more ditches. A tabulation of trap spacing and grid area (Table 4) demonstrates these conditions in the four grids. A mean figure for trap spacing was arrived at by measuring the distances between the upper and lower trap rows at the first, fifth, and ninth traps, and deriving an average, for each grid. Acreage (used in population density estimates) is based on an added boundary strip of 100 ft, an approximate equivalent of av. D.

Table 5 compares for mice the two measures of ARL in Field 001. Numbers of moves between ditches increase as frequency of capture increases, and the maximum effect of this is in Class IV, with five or more captures and survival of 5 or more months. Data on mice caught not more than twice and surviving only 2 months (Class I) are not totally rejected. This is the largest class, which emphasizes rapid loss of mice from the population and a high replacement rate. All mice were at least 4 to 6 weeks old when first caught, and were assumed to have survived 2 months or more if caught in any month succeeding original capture. Therefore, age and survivorship are realistically similar to known lengths of residence in the trap complexes. Data on age, survivorship, or residence are presented in this paper for general comparative purposes, and are not intended as accurate portrayals of rates of longevity.

TABLE 5

MEAN ADJUSTED RANGE LENGTHS (ARL) IN FEET FOR *Mus musculus,* IN IRRIGATED SUGAR CANE, FIELD 001
(Range lengths are plotted by capture and survival class, and in relation to placement of trap rows: L, all captures in one row along a contour ditch; NL, captures in two or more rows)

CAPTURE AND SURVIVAL CLASS	SEX	RANGE ORIENTATION	(n)	MEAN NUMBER OF CAPTURES	MEAN MONTHS OF SURVIVAL	MEAN ARL	EXTREMES OF ARL
I	M	L	96	2.7	2.4	127	50–400
2–4 captures,		NL	71	2.9	2.6	229	85–525
2–4 months survival	F	L	113	2.7	2.5	118	50–400
		NL	59	2.8	2.6	204	100–490
	Summary		339	2.73	2.50	158	50–525
II	M	L	30	5.6	3.3	187	50–350
5 or more captures,		NL	29	6.0	3.3	237	100–415
2–4 months survival	F	L	13	6.2	3.4	162	100–400
		NL	9	5.2	3.1	211	130–330
	Summary		81	5.80	3.29	203	50–415
III	M	L	5	3.4	5.2	150	50–300
2–4 captures, 5 or		NL	2	2.5	7.5	228	225–230
more months survival	F	L	6	3.5	5.8	167	50–250
		NL	5	3.2	5.6	315	180–600
	Summary		18	3.27	5.77	210	50–600
IV	M	L	15	7.9	6.2	218	100–350
5 or more captures,		NL	20	8.4	6.5	278	140–455
5 or more months	F	L	9	7.1	6.0	178	100–250
survival		NL	21	9.7	7.5	307	155–600
	Summary		65	8.52	6.67	260	100–600

Number of captures and months of survival are directly related, as seen in cross-comparisons of summaries in Classes I and IV, and II and III. The small size of Class III is a further indication that mice are readily trapped as long as they range in the trapping area. There is progressive lengthening of ARL with time. The survivors become fewer, but they continue to be caught, and movements of greater lengths are recorded, partly through shifts in individual ranges. Thus, the potential maximum range length may be demonstrated by few individual animals. Variable grid size in Field 001, and the consequent greater spacing between trap rows in Grid III (the largest), tended to result in longer NL measures in this grid, and this seems to be simply because the mice had to move farther in order to reach traps on different ditches.

In choosing criteria for expressing near-maximum ARL for rodents, data based on few captures over a short period of time are usually excluded. Hence, in all summary statements, Class I records are omitted. Table 6 presents results for *M. musculus* in all study areas. In summary, for males ARL is 228 ft, and for females, 219 ft. Extremes in all habitats are 50 and 600 ft. The maximum of 600 ft is considerably less than the possible 785 ft in the largest grid.

Grid sizes, therefore, were large enough to demonstrate probably true measures of range length. In Field 101b at Kukuihaele (50-ft × 50-ft grids), for males it was 243 ft compared with 227 ft in Field 001, and in 101b Gulch (35-ft × 50-ft grids), 194 ft; in the sparsely populated Spencer Field–Field 33b complex it was 241 ft. Measures for females were comparable, and as is the case with other measures of movement, generally shorter.

Kukuihaele data were not subjected to the elaborate analyses given those from Field 001. It is easily observed, however, that ARL figures determined under dissimilar grid styles, were almost identical. The exceptionally small figures from 101b Gulch may reflect an actual marked sedentariness in this circumscribed habitat, rather than close spacing of traps. Because of the marked similarity of ARL figures by sex and habitat, and small size of sample in some cases, the rank test was not applied to them.

DISPERSAL: The grids were not necessarily superior to check lines in determining adjusted range lengths. The line in Kukui Gulch was of particular interest because of its nearness to Field 001, Grid I, and Grid III. During the first 4 months of the study 67 mice were marked in the gulch; afterward, only 30 were marked, and 20 of these were first caught in November–December 1960. The first population disappeared, or dispersed to the cane as it

TABLE 6

ADJUSTED RANGE LENGTHS (ARL) IN FEET, FREQUENCY OF CAPTURE, AND SURVIVAL IN MONTHS, FOR *Mus musculus*, BY SEX AND FOR THE SEVERAL HABITATS
(Classes II, III, and IV of Table 5 are combined)

SITE	SEX	(n)	MEAN NUMBER OF CAPTURES	MEAN MONTHS OF SURVIVAL	MEAN ARL	EXTREMES OF ARL
Field 001	M	101	6.4	4.5	227	50–455
50 × 50+-ft grids	F	63	6.9	5.5	232	50–600
Field 101b	M	35	6.0	4.5	243	100–455
50 × 50-ft grids	F	24	5.8	4.7	227	100–480
101b Gulch	M	6	4.3	5.0	194	70–315
35 × 50-ft grids	F	7	4.2	5.5	146	85–175
Spencer Field	M	5	3.4	4.4	241	150–320
and Field 33b	F	10	3.9	5.9	202	100–380
50 × 50-ft grids						
Summary	M	147	6.14	4.53	228	50–455
	F	104	6.17	5.37	219	50–600

developed, and the second one apparently came from the cane when numbers there were high. Otherwise, in 14 of the 20 months, Kukui Gulch was almost totally unattractive to mice. Only 9 mice marked in the cane field were recaptured in the gulch, and just 10 gulch mice were recaptured in the cane. Mean ARL for these 19 animals was 453 ft, ranging from 230 to 756 ft. This large figure suggests a restive tendency among mice that occupied both habitats. A total of 18 mice caught more than once in the gulch only had a mean ARL of 244 ft (range 50–750), comparable to that in the field. Of this total of 37 animals, 4 in the gulch and 5 in both cane and gulch were caught 5 or more times, demonstrating that the mixed habitat was the regular residence of at least some mice.

Movement between grids was surprisingly uncommon, with only 8 records in the 20-month study of Field 001. Minimal distances between traps of adjacent grids ranged from 560 to 1,525 ft, and the maximal distances ranged from 1,530 to 2,625 ft, or about 0.3 to 0.5 mile. These 8 mice moved from 1,015 to 2,020 ft, for an average distance of 1,636 ft. No mouse that moved to a second grid was again captured in the first one. This evidence reinforces the idea that *M. musculus* is a generally sedentary animal and that long sorties from its usual home are few. The various dispersive moves, between grids and from Field 001, are shown in Figure 7.

Two adult males moved from Kukui Gulch to Grid IV at the far side of Field 001, one traveling 1,780 ft from the point of previous capture, and the other, 2,665 ft. One female moved up Kukui Gulch for 1,950 ft, although

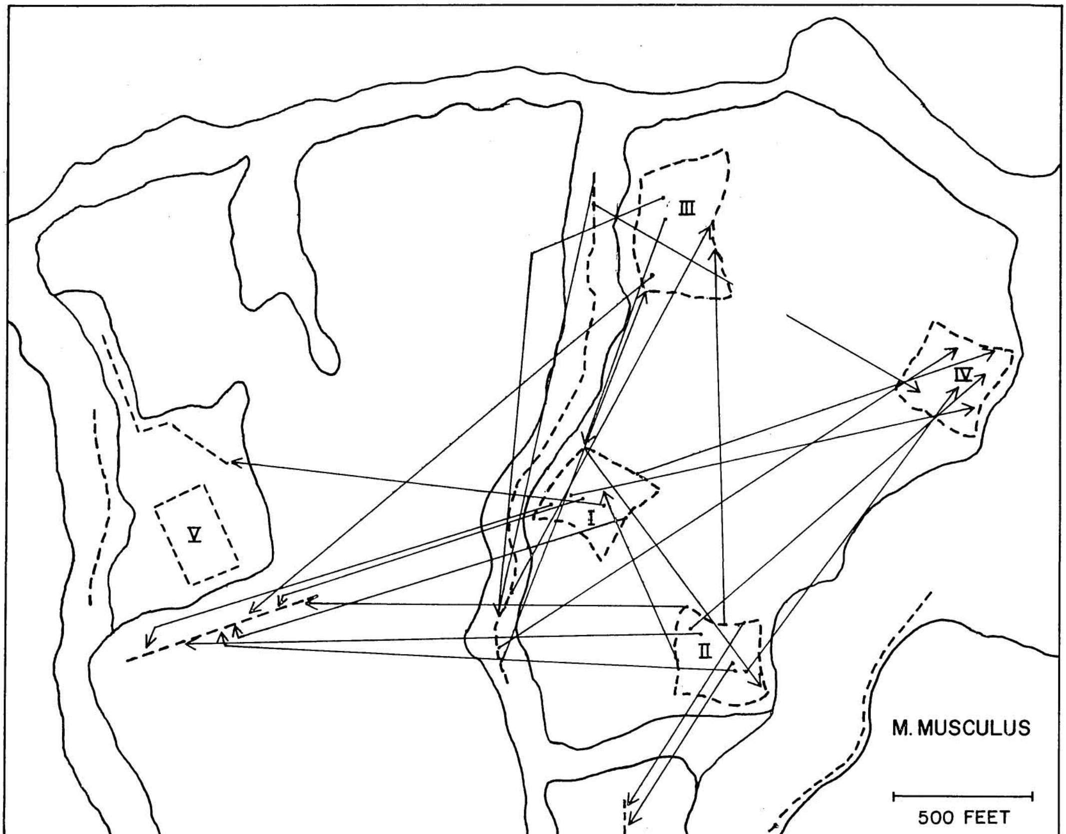

FIG. 7. Dispersive moves of *Mus musculus,* 1959–61, within and from the Field 001 trap complex. The various trap grids and trap lines are marked by dashed lines. Compare with Figure 1.

this was not a usual route of movement, even among gulch residents. One male moved 1,580 ft from Grid III into the gulch.

The longer dispersive moves often carried mice out of the Field 001 area. Kahaupu Gulch and the sea cliffs were apparently almost absolute barriers to movement, but adjacent Fields 17 and 33b attracted possibly dozens of mice. Monthly trapping in these fields and in Spencer Field revealed a clear pattern of dispersal from Field 001. Eleven of these mice were recovered. Two moved to Field 17, 8 to Field 33b, and 1 to Spencer Field. The grassland of Spencer Field and its adjacent Ouhi Gulch seemed to have a barrier effect which guided mice to the arm of Field 33b where a snap-trap line was located at that time. Ouhi is intermediate in depth and width between the two gulches bordering Field 001. No mice were recovered in the Field 20 line, 0.5 mile beyond Ouhi Gulch. Six of the 11 were males, and these 6 dispersed an average of 2,195 ft; for the 5 females the figure was 1,726 ft. The range among these moves was not large and was governed in part by distances between the trap complexes. One mouse, established from September to November 1960 in the check line at the far side of Kahaupu Gulch, appeared in December, 21 days after its previous capture, in Field 33b, 3,020 ft away. Otherwise Kahaupu was a distinct barrier to movement, and no other mice were known to have crossed it. Also, no mice were recovered from Field 006, two deep gulches removed from Field 001, east of the Paauhau Mill.

The mean elapsed time between previous capture and recovery of 25 mice considered to have dispersed within the Field 001 area was 56 days (range 5–236 days), with no particular trends related to age or sex. Most recoveries of dispersed mice occurred in Time Period III of the crop cycle, after the peak population of 24 mice per acre had been reached in Field 001. Again, there was no particular trend related to age or sex, except that early in the crop when the population was largely adult (Period I) no dispersed young were recovered. In Period II, 3 young mice were recovered. When the main dispersal took place (Period III), only 5 adults were recovered to 10 young. Apparently few mice dispersed in Period IV, because none was recovered. As the population level rose again in Period V, there were 2 more recoveries, 1 adult and 1 young. Dispersal distances for the 25 mice ranged from 1,015 to 2,850 ft, averaging 1,941 ft for males and 1,743 for females.

At Kukuihaele, mouse dispersal was usually not easily distinguishable from longer in-range movements, because of closer spacing of grids and trap lines. In all, 21 males ranged in both cane-field grids, or to the Kukuihaele Gulch snap-trap line. Of these patterns, 15 appeared to be longer range lengths in which the mouse stayed usually in a more restricted home area. Six seemed to represent dispersal, averaging 803 ft. Fifteen females were caught in two or more grids or lines, with three examples considered to be dispersal and averaging 947 ft.

Dispersive moves of more than 0.5 mile must be uncommon, although the chances of catching a rodent decrease rapidly with distance dispersed because of the increasingly large peripheral area available to a moving animal. Virtually continuous trapping in and around Kukuihaele Village, by rodent control crews, yielded no marked mice. The monthly operation of the five lines in cane fields above the grids yielded only 1 marked mouse. It had moved from Grid V to Field 123, a distance of nearly 8,000 ft, in 13 days or less. This is a remarkable record, but because it is unique, it has little significance in the overall pattern of mouse movement.

Rattus exulans

LOCAL MOVEMENT: The Polynesian rat is well distributed to all habitats studied, and was ordinarily numerous enough to provide useful quantitative data. The measure av. D was applied to these as it was applied to the mouse data. In summary, av. D for males was 82 ft, and for females it was 70 ft, among repeats; for returning males the figure was 113 ft, and for like females, 91 ft. Table 7 presents comparative data from all habitats. Seeming differences in av. D between habitats and in relation to trap arrangement are more conspicuous, and perhaps more real, than for *M. musculus*. The grassland of Spencer Field and the cane land of Field 33b have the most mobile populations, with av. D as long as 163 and 191

TABLE 7

AVERAGE DISTANCE IN FEET BETWEEN CAPTURES (av. D) AND RATE BY PERCENTAGE OF RECAPTURE IN TRAP OF PREVIOUS CAPTURE (% D = 0), FOR *Rattus exulans*, AT TWO LEVELS OF ELAPSED TIME AND UNDER VARIOUS ARRANGEMENTS OF TRAPS, BY SEX AND IN VARIOUS HABITATS

	REPEAT WITHIN 4-DAY TRAPPING PERIOD (R)						RETURN AFTER ONE OR MORE MONTHS (R1)						P VALUES FROM RANK TEST OF av. D			
	M (a)			F (b)			M (c)			F (d)						
SITE	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0	(ab)	(cd)	(ac)	(bd)
Field 001 50 × 50+-ft grids	94	(20)	30.0	69	(52)	23.1	102	(25)	12.0	83	(86)	19.8	.350	.131	.224	.180
Field 101b 50 × 50-ft grids	79	(75)	21.3	51	(68)	27.9	93	(56)	8.9	79	(84)	19.0	.030*	.099	.044*	.006**
101b Gulch 35 × 50-ft grids	61	(52)	28.8	64	(71)	19.7	70	(66)	15.2	70	(81)	24.7	.221	.375	.176	.224
Kukui and Kahaupu 50-ft gulch lines	74	(123)	39.8	43	(87)	55.2	77	(79)	35.4	53	(134)	47.8	.008**	.028*	.242	.108
Spencer Field 50 × 50-ft grid	96	(94)	11.8	86	(77)	16.7	191	(63)	11.1	188	(63)	3.2	.334	.397	.000**	.000**
Field 33b 50 × 50-ft grid	97	(49)	30.6	113	(51)	11.8	163	(39)	10.3	139	(45)	17.8	.115	.159	.001**	.057
Summary	82	(413)	27.3	70	(406)	27.5	113	(328)	17.4	91	(493)	25.8	.117	.004**	.000**	.001**

* Significant ($P < .05$).
** Highly significant ($P < .01$).

TABLE 8

AVERAGE DISTANCE IN FEET BETWEEN CAPTURES (av. D) AND PERCENT OF EXAMPLES IN EACH CLASS (%) FOR *Rattus exulans*, BY TIME INTERVAL IN MONTHS SINCE PREVIOUS CAPTURE AND BY SEX, FOR THE SEVERAL STUDY PLOTS

	NUMBER OF MONTHS SINCE PREVIOUS CAPTURE											
	1			2			3			4 or more		
SITE	av.D	(n)	%	av.D	(n)	%	av.D	(n)	%	av.D	(n)	%
Field 001 and Field 101b												
M	95	(54)	66.7	111	(13)	16.0	81	(7)	8.6	63	(7)	8.6
F	76	(100)	58.8	77	(47)	27.6	114	(10)	5.9	99	(13)	7.6
Kukui Gulch and Kahaupu Gulch												
M	42	(53)	67.1	90	(5)	6.3	94	(8)	10.1	100	(13)	16.5
F	37	(83)	61.9	69	(35)	26.1	100	(4)	3.0	100	(12)	9.0
101b Gulch												
M	57	(43)	65.2	113	(12)	18.2	86	(3)	4.5	74	(8)	12.1
F	70	(56)	69.1	94	(12)	14.8	48	(4)	4.9	44	(9)	11.1
Spencer Field												
M	156	(46)	73.0	284	(11)	17.5	111	(1)	1.6	327	(5)	7.9
F	169	(50)	79.4	221	(9)	14.3	216	(1)	1.6	396	(3)	4.8
Field 33b												
M	164	(28)	71.8	216	(5)	12.8	100	(2)	5.1	124	(4)	10.3
F	143	(34)	75.6	95	(7)	15.6	–	(0)	–	179	(4)	8.9
Summary												
M	96	(224)	68.3	162	(46)	14.0	90	(21)	6.4	121	(37)	11.3
F	86	(323)	65.5	89	(110)	22.3	102	(19)	3.9	117	(41)	8.3

ft in rats recaptured after a month or more. In contrast, rats in Kukui Gulch and in Kahaupu Gulch demonstrated highly restricted movement.

Rank tests by sex and time within habitat reveal a generally variable pattern of significant differences. Repeating males were more mobile than repeating females (*ab*) in both Field 101b grids and in the gulch lines. In summary of *ab,* however, there was no significant difference between the figures of 80 ft for males and of 70 ft for females. In further summary, highly significant differences were demonstrated between male and female returns (*cd*), and between male repeats and returns (*ac*) and their female counterparts (*bd*).

Rates of return to the same trap on successive captures were moderate but variable (% D = 0, in Table 7). In the grids, for the 4-day trapping period, the rate is about 25 percent in each sex. In the gulch lines the figures were consistently high at 35 to 55 percent. Overall, *R. exulans* is recaught in the trap of previous capture about once in four times, except for males that return after a month or more. For these, the rate drops to about once in six captures.

Table 8 shows in detail the distribution of recaptured rats in time. The Polynesian rat was quite easily captured, for some 67 percent of recaptures occur in the month following a previous capture; about 85 percent occur within 2 months. Because a moderate number of these rats are long lived, more were tallied in the 4-or-more-months class than in the 3-months class. Av. D shows no dramatic changes with time elasped between captures, but in general there is an increase in its length.

Growth and development of sugar cane, and the related changes in rodent population densities (Fig. 5), have a moderate effect on av. D in *R. exulans.* Early in the crop cycle, this rat was scarce, especially in Field 001 (Table 9), and so data are few. However, there is an evident trend for a longer av. D during Time Period I in this field and in Field 101b. This trend extends into Period II only in Field 001. Figures for % D = 0 are relatively low in both

TABLE 9

AVERAGE DISTANCE IN FEET BETWEEN CAPTURES (av. D) AND RATE BY PERCENTAGE OF RECAPTURE IN THE TRAP OF PREVIOUS CAPTURE (% D = 0), FOR *Rattus exulans*, DURING FIVE 4-MONTH GOWTH PERIODS IN THE CROP CYCLE OF THREE SUGAR CANE FIELDS

	GROWTH PERIOD AND AGE OF CANE IN MONTHS														
	I 3–6			II 7–10			III 11–14			IV 15–18			V 19–22		
SITE	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0	av.D	(n)	%D=0
Field 001	136	(7)	7.1	222	(6)	0	89	(18)	5.6	68	(33)	27.3	66	(82)	28.0
Field 101b	110	(15)	13.3	82	(54)	13.0	76	(43)	18.6	69	(49)	22.4	72	(61)	27.9
Field 33b	103	(29)	20.7	49	(10)	20.0	119	(32)	12.5	162	(19)	5.3	184	(15)	13.3
Summary	110	(51)	17.6	90	(70)	12.9	93	(93)	14.0	87	(101)	20.8	80	(158)	26.6

fields until Periods IV and V, when they reach the usual level of about one in four captures in the trap of previous capture. Cane is then 15 to 22 months old, and population densities are increased. Rats in Field 33b demonstrated a generally increasing av. D throughout the cane cycle, accompanied by decreasing frequency of successive capture in the same trap, and correlated with a consistently low population density.

HOME RANGE: Criteria for adjusted range length are the same as those applied to data on *M. musculus*. In Field 001 under the special conditions imposed by the contour irrigation channels, linear and nonlinear figures were available, but it was necessary to combine several classes of them in order to secure meaningful results (Table 10). Linear ranges along the ditches were consistently shorter than the nonlinear ranges that included one or more traps on an adjacent ditch. Females tended to have greater survival than males, and were caught more frequently, but ranges of males were longer. Mean captures and mean survival increased together, and ranges were longer for rats caught repeatedly with increase of time. Overall, the data for Classes II to IV show a mean ARL of 225 ft, with extremes at 100 and 450 ft.

Table 11 summarizes data for all the study plots. Three pairs of plots, Fields 001–101b, the gulch grids and lines, and the Spencer Field–Field 33b complex, each have mean ARL figures that are remarkedly similar for each sex. This suggests that the various arrangements of traps in grids or rows, and spacing of traps, had possibly no adverse effects on results. It appears, then, that true differences in ARL are reflections of the environment, including the physical surroundings and relative densities of rodent populations. Rank tests of these data, combined for the paired habitats and segregated by sex, reveal these differences. Four of the six pairs are highly significantly different, one pair is significantly different, and one demonstrates no significant difference (Table 12).

DISPERSAL: It is impossible to distinguish between exceptionally long moves within the home range and moves of dispersal; indeed, most records of marked rats are insufficiently complete to reveal the exact range occupied by the individual rat. *R. exulans* makes occasional moves away from its usual range, and returns home; perhaps these are ordinary daily moves, but trapping reveals them rather infrequently. Such moves account for most range lengths longer than 400 ft.

In Field 001 there were several such records, the rat in each case associated with the adjacent Kukui Gulch. In February 1960 a juvenile fe-

TABLE 10

MEAN ADJUSTED RANGE LENGTHS (ARL) IN FEET FOR *Rattus exulans*, IN IRRIGATED SUGAR CANE, FIELD 001
(Range lengths are plotted by capture and survival class, and in relation to placement of trap rows: L, all captures in one row along a contour ditch; NL, captures in two or more rows)

CAPTURE AND SURVIVAL CLASS	SEX	RANGE ORIENTATION	(n)	MEAN NUMBER OF CAPTURES	MEAN MONTHS OF SURVIVAL	MEAN ARL	EXTREMES OF ARL
I	M	L	12	2.2	2.4	121	50–200
2–4 captures,		NL	8	2.4	2.6	202	125–300
2–4 months survival	F	L	36	2.4	2.9	115	50–350
		NL	12	2.8	2.9	190	120–255
Summary			68	2.44	2.77	140	50–350
II, III, IV	M	L	1	2.0	5.0	100	100–100
2–5 or more captures,		NL	2	3.5	4.5	340	275–450
2–5 or more months survival	F	L	5	2.8	5.4	130	100–295
		NL	11	5.1	5.5	259	150–400
Summary			19	4.15	5.31	225	100–450

TABLE 11

ADJUSTED RANGE LENGTHS (ARL) IN FEET, FREQUENCY OF CAPTURE, AND SURVIVAL IN MONTHS, FOR *Rattus exulans*, BY SEX AND FOR THE SEVERAL HABITATS
(Classes II, III, and IV of Table 5 are combined)

SITE	SEX	(n)	MEAN NUMBER OF CAPTURES	MEAN MONTHS OF SURVIVAL	MEAN ARL	EXTREMES OF ARL
Field 001	M	3	3.0	4.7	260	100–450
50 × 50+-ft grids	F	16	4.4	5.4	219	100–395
Field 101b	M	14	4.4	5.1	277	100–720
50 × 50-ft grids	F	16	5.4	5.9	210	100–315
101b Gulch	M	17	5.0	6.4	227	35–735
35 × 50-ft grids	F	19	5.2	6.2	160	35–520
Kukui and Kahaupu	M	26	4.6	4.8	222	50–550
50-ft gulch lines	F	24	5.0	7.1	165	50–400
Field 33b	M	13	6.2	5.3	334	120–600
50 × 50-ft grid	F	10	6.1	5.1	312	165–590
Spencer Field	M	18	4.8	4.6	339	150–600
50 × 50-ft grid	F	16	6.1	5.6	319	190–570
Summary	M	91	4.86	5.16	272	35–735
	F	101	5.26	6.01	219	35–590

male marked in Grid III moved 195 ft to the gulch; then it was trapped in Grid I before the end of that month. In June and again in September it was recorded again in Grid III as a reproductive adult. The ARL was 925 ft. Two males in March and April 1960 made similar patterns of movement in the gulch and grid, registering ARL figures of 875 and 630 ft. Actual dispersal seems to have occurred in an adult rat that was tagged in June 1960 in Kukui Gulch. In July and in the following January it was recaptured in Grid II, having moved 1,015 ft from the point of original capture. A juvenile gulch rat marked in March 1961 was recovered 2 months later as a young adult, diagonally across Field 001 and 2,030 ft

TABLE 12

PROBABILITIES OF DIFFERENCES IN ADJUSTED RANGE LENGTHS (ARL) OF *Rattus exulans* FROM RANK TESTS, BY LIKE SEX AND FOR THE SEVERAL HABITATS

	KUKUI, KAHAUPU, AND 101b GULCHES						SPENCER FIELD, FIELD 33b					
SITE	M ARL	(n)	P	F ARL	(n)	P	M ARL	(n)	P	F ARL	(n)	P
Field 001 Field 101b												
M	224 274	(43) (17)	.140				337 274	(31) (17)	.050*			
F				163 215	(43) (32)	.005**				317 215	(26) (32)	.000**
Spencer Field Field 33b												
M	224 337	(43) (31)	.003**									
F				163 317	(43) (26)	.000**						

* Significant (P < .05).
** Highly significant (P < .01).

away, in Grid IV. An adult female that lived on the rim of Kahaupu Gulch in September 1961 and last seen there in December, moved 5,500 ft away from the study area, across adjacent cane land to Kahawailiilii Gulch, where it was recovered in February 1962 in routine trapping by rodent control personnel. No *R. exulans* were known to travel between the Field 33b grids and Field 001, or to Field 17.

In the Kukuihaele study area, with similar opportunities for capturing rats, the pattern was like that at Paauhau. Thirteen males ranged between separated grids or to the snap-trap line that crossed from Field 101b to Field 111, for a mean adjusted range length of 495 ft. Two others appear to have moved 430 and 920 ft, respectively. One rat definitely left the trap area and was recovered some weeks later in a brushy pasture below Kukuihaele Village, 1,720 ft from the point of previous capture. An immature male marked in Grid VIII in May 1961 was caught the following February in the Field 121 snap-trap line at the rim of Waipio Valley, 7,300 ft away, at an elevation 900 ft higher than Grid VIII. It is significant that the five trap lines above the grid area caught only this one marked rat in 5 full years of operation, at 4 days per month.

A remarkable trait of behavior in *R. exulans,* and this may apply similarly to all the species studied, is that it almost always keeps the individual in a restricted home area. Surely, if there were high frequencies of dispersal and life-long vagrancy in these rodents, many more marked animals would have been intercepted in the more distant trap lines and grids.

Rattus rattus

The roof rat was common in the gulches and in grassland. Most data come from 101b Gulch, where the two grids were in undisturbed operation for 5 years. The few cane-field records collected are combined with those from adjacent gulches. Comparisons of data from Paauhau with those from Kukuihaele are essentially comparisons of results from the gulch check lines with those from 101b Gulch grids.

LOCAL MOVEMENT: Av. D was consistently longer in Spencer Field and in Field 33b than in other areas (Table 13), following a pattern similar to that for *R. exulans*. In several cases the data appear to be significantly different between habitats. The Wilcoxon's rank test was confined to arrays comparing differences related to sex and to time elapsed between captures, within habitats, in the same manner as for *M. musculus* and *R. exulans*. For Field 33b, where all samples were small, none of the pairs was statistically distinct. In 101b Gulch, where samples were larger, three of the four pairs of data were statistically different. In summary, av. D for males was significantly longer than for females among repeats (*ab*), at 90 and 73 ft, and highly significantly different by sex among returns (*cd*), at 132 and 86 ft. Male returns had highly significantly longer av. D than did repeats (*ac*), and for females the difference was significant (*bd*).

Rats entered the same trap on successive captures in a variable fashion (Table 13). The rate (% D = 0) was particularly high among the several records from the gulches bordering Field 001 and for the few records in this field, about one out of two captures among rats repeating capture in the 4-day trapping period, for both sexes. Among rats returning to the traps after a month or more, the rate fell to about one in four captures for males, and to one in three for females. In all other areas, namely, the 35-ft × 50-ft grids in 101b Gulch and the 50-ft × 50-ft grids of the Spencer Field–Field 33b complex, rats returned to a trap of previous capture only about once in 10 times.

By numbers of months between captures (Table 14) a fairly firm pattern emerges for lengths of av. D. In males the trend is toward increase with time, and in females it remains about the same. Some 53 percent of all *R. rattus* recaptured were caught in the first month after a previous capture, and about 73 percent were caught by the second month, revealing a moderate positive response to the traps, if the individual, once marked, was susceptible to recapture. As with *R. exulans,* the 3-months time class contained fewer examples than did the succeeding class, again expressing greater longevity than *M. musculus*.

Because nearly all records of *R. rattus* are from habitats other than sugar cane, seasonal rates of capture and lengths of movements were classed by quarters of the year instead of

TABLE 13

AVERAGE DISTANCE IN FEET BETWEEN CAPTURES (av. D) AND RATE BY PERCENTAGE OF RECAPTURE IN TRAP OF PREVIOUS CAPTURE (%D=0), FOR *Rattus rattus*, AT TWO LEVELS OF ELAPSED TIME AND UNDER VARIOUS ARRANGEMENTS OF TRAPS, BY SEX AND IN VARIOUS HABITATS

	REPEAT WITHIN 4-DAY TRAPPING PERIOD (R)						RETURN AFTER ONE OR MORE MONTHS (R1)						P VALUES FROM RANK TEST OF av. D			
	M (a)			F (b)			M (c)			F (d)						
SITE	av. D	(n)	%D=0	av. D	(n)	%D=0	av. D	(n)	%D=0	av. D	(n)	%D=0	(ab)	(cd)	(ac)	(bd)
Kukui Gulch, Field 001 and Kahaupu Gulch	53	(29)	48.3	36	(39)	53.8	87	(43)	27.9	62	(56)	33.9	.236	.053	.045*	.041*
101b Gulch 35 × 50-ft grids	92	(95)	10.5	71	(113)	9.7	97	(141)	11.3	85	(170)	11.2	.121	.000**	.001**	.033*
Spencer Field 50 × 50-ft grid	102	(40)	7.5	109	(30)	10.0	161	(56)	8.9	125	(33)	12.1	.409	.067	.006**	.271
Field 33b 50 × 50-ft grid	114	(14)	7.1	121	(12)	16.7	135	(10)	0	135	(10)	0	.375	.394	.268	.448
Summary	90	(178)	15.7	73	(194)	19.0	132	(250)	13.8	86	(269)	16.2	.040*	.000**	.000**	.022*

* Significant ($P < .05$).
** Highly significant ($P < .01$).

TABLE 14

AVERAGE DISTANCE IN FEET BETWEEN CAPTURES (av. D) AND PERCENT OF EXAMPLES IN EACH CLASS (%) FOR *Rattus rattus*, BY TIME INTERVAL IN MONTHS SINCE PREVIOUS CAPTURE AND BY SEX, FOR THE SEVERAL STUDY PLOTS

	NUMBER OF MONTHS SINCE PREVIOUS CAPTURE											
	1			2			3			4 OR MORE		
SITE	av. D	(n)	%	av. D	(n)	%	av. D	(n)	%	av. D	(n)	%
All sites (except below)												
M	116	(95)	51.6	80	(37)	20.1	126	(23)	12.5	187	(29)	15.8
F	75	(118)	52.2	80	(39)	17.3	91	(19)	8.4	82	(50)	22.1
Spencer Field and Field 33b												
M	146	(44)	66.7	178	(13)	19.7	119	(3)	4.5	213	(6)	9.1
F	137	(19)	46.2	126	(13)	25.6	108	(4)	10.3	117	(7)	17.9
Summary												
M	126	(139)	55.6	106	(50)	20.0	125	(26)	10.4	191	(35)	14.0
F	84	(137)	50.9	92	(52)	19.3	94	(23)	8.6	86	(57)	21.2

growth periods of sugar cane that were employed for *M. musculus* and *R. exulans,* in order to display possible behavioral changes during the year (Table 15). The undisturbed gulch and grassland habitats were physically much more stable than were the cane fields. No distinct pattern emerged to indicate forceful seasonal changes in rat movement, although in the third and fourth quarters av. D is generally shorter than in other quarters. Rate of return to the trap of previous capture (% D = 0) is generally inverse to length of av. D, and this is best exemplified by data from the Kukui Gulch area.

Adjusted range lengths were not greatly variable between sexes or between habitats (Table 16). Mean numbers of captures and mean months of survival suggest relative stability in the *R. rattus* populations. One reason for the rather uniform expression of ARL seems to be that most rats were confined to the gulch and grassland habitats, and did not venture to any extent from habitat to habitat. Rank tests of ARL, by like sex and between habitats (Table 17) reveal that Spencer Field area females had highly significantly longer ranges, at 269 ft, than had those in the Kahaupu Gulch area at 174 ft, and significantly longer ranges than those of the 101b Gulch area at 198 ft. The other four pairs of figures tested were not statistically different.

DISPERSAL: *R. rattus* rarely moves away from its home area. Only 13 males and 3 females ranged in two grids or between a grid and a line of traps. Seven males from the Kukuihaele area apparently changed their home stations, but in so doing moved an average of only 546 ft, with a maximum of only 686 ft by one individual. The longest move among females, from one station to another in the Kukuihaele area, was 364 ft, but this could not be considered a dispersive move. These figures for both sexes are all tallied as ordinary expressions of range length. Similarly, in the Paauhau area there were no examples that suggested dispersal.

Rattus norvegicus

The Norway rat was rapidly declining in numbers when the investigations began in 1958. The last one was marked in the field in March 1961, and the final capture of this species was in May of the same year. In 1964 occassional rats were again caught in the system of snap-trap lines, and small populations remained in and about some of the villages and farmsteads throughout the years of the project.

When present in the study areas, *R. norvegicus* was sparsely distributed to all habitats without obvious preference. In Field 001 it was plain that this species was closely associated with stone piles at the edge of Grid I. This

TABLE 15

AVERAGE DISTANCE IN FEET BETWEEN CAPTURES (av. D) AND RATE BY PERCENTAGE OF RECAPTURE IN THE TRAP OF PREVIOUS CAPTURE (%D=0), FOR *Rattus rattus*, DURING QUARTERLY PERIODS OF THE YEAR, IN ALL HABITATS

	QUARTER											
	I JAN–MAR			II APR–JUNE			III JULY–SEPT			IV OCT–DEC		
SITE	av. D	(n)	%D=0	av. D	(n)	%D=0	av. D	(n)	%D=0	av. D	(n)	%D=0
Kukui Gulch Area	53	(15)	33.3	50	(41)	41.5	23	(17)	64.7	61	(38)	39.5
101b Gulch Area	103	(88)	6.8	92	(85)	12.9	83	(42)	14.3	69	(110)	10.0
Spencer Field Area	120	(21)	9.5	120	(37)	16.2	126	(41)	4.9	106	(39)	10.3
Summary	99	(124)	10.5	88	(163)	20.9	91	(100)	19.0	75	(187)	16.0

TABLE 16

ADJUSTED RANGE LENGTHS (ARL) IN FEET, FREQUENCY OF CAPTURE, AND SURVIVAL IN MONTHS, FOR *Rattus rattus*, BY SEX AND FOR THE SEVERAL HABITATS

(Classes II, III, and IV of Table 5 are combined)

SITE	SEX	(n)	MEAN NUMBER OF CAPTURES	MEAN MONTHS OF SURVIVAL	MEAN ARL	EXTREMES OF ARL
Kukui Gulch Area	M	10	3.0	7.1	205	50–450
	F	17	4.5	7.1	174	50–550
101b Gulch Area	M	31	5.0	6.9	233	85–455
	F	45	5.5	8.4	198	70–365
Spencer Field Area	M	11	6.5	5.4	266	50–545
	F	11	5.4	7.6	269	100–370
Summary	M	52	4.92	6.63	235	50–545
	F	73	5.26	8.00	203	50–550

colony died out before the end of the 1959–61 crop cycle.

MOVEMENT PATTERNS: The Norway rat appears to have movement patterns similar to those of the other species studied (Table 18). Av. D is relatively large and the rate of return to the trap of previous capture is low, as might be expected in a low-density population. Mean captures were fewer than three for each sex; females apparently survived longer than did males. Only 2 rats made what seemed to be dispersive moves, a male for 715 ft, and a female for 2,600 ft.

Effects of Manipulating the Environment

Changes in the environment, whether cyclic, seasonal, periodic, gradual, or abrupt, may have profound influences on rodent populations. In the study areas, sugar cane is harvested at intervals of 20 to 24 months, and replanted usu-

TABLE 17

PROBABILITIES OF DIFFERENCES IN ADJUSTED RANGE LENGTHS (ARL) OF *Rattus rattus* FROM RANK TESTS, BY LIKE SEX AND FOR THE SEVERAL HABITATS

	101b GULCH AREA						SPENCER FIELD AREA					
SITE	M ARL	(n)	P	F ARL	(n)	P	M ARL	(n)	P	F ARL	(n)	P
Kahaupu Gulch Area												
M	233	(31)	.125				266	(11)	.087			
	205	(10)					205	(10)				
F				198	(45)	.054				269	(11)	.008**
				174	(17)					174	(17)	
Spencer Field Area												
M	233	(31)	.200									
	266	(11)										
F				198	(45)	.015*						
				269	(11)							

* Significant ($P < .05$).
** Highly significant ($P < .01$).

TABLE 18

SUMMARY OF DATA ON MOVEMENTS OF *Rattus norvegicus*, IN ALL STUDY AREAS

	AVERAGE DISTANCE BETWEEN CAPTURES (av. D) IN FEET			
	M		F	
	(n)	av. D	(n)	av. D
Repeat within 4-day trapping period	20	159	10	208
Return after one or more months	20	216	23	135
	RATE BY PERCENTAGE OF RECAPTURE IN TRAP OF PREVIOUS CAPTURE (%D=0)			
	M		F	
	(n)	%D=0	(n)	%D=0
All examples of D	40	10.0	33	6.1
	MEAN ADJUSTED RANGE LENGTH (ARL), IN FEET			
	M		F	
	(n)	ARL	(n)	ARL
Classes I–IV* combined	17	286	17	216
	RATE OF CAPTURE (C)			
	M		F	
	(n)	C	(n)	C
Mean numbers of captures	17	2.7	17	2.8
	RATE OF SURVIVAL (S)			
	M		F	
	(n)	S	(n)	S
Mean survival in months	17	2.8	17	4.8

* See Table 5 for criteria.

ally after each third crop. Mechanical harvest completely devastates the surface habitat and deep plowing that precedes planting obliterates nest chambers and burrows. The standing mature cane is usually burned in blocks of several acres as harvest proceeds in a field, to remove accumulated litter, weeds, and foliage. Fire itself seems not to be dangerous to rodents because even a thin layer of soil is protective against it. Large tractors equipped with heavy buck rakes skim off the tangled cane and push it into windrows or piles for loading. Finally the field is worked with a light drag rake to recover essentially all remnants of broken or loose cane stalks. Ditches, lanes, and cultivation furrows are obliterated, leaving the field surface smooth and bare. Various heavy equipment churns and packs much of the surface layers of soil to depths of a foot or more. Harvest is often continuous, day and night, once it has begun, leaving the rodents little respite in which to flee from the catastrophe.

It would seem that many rodents could survive underground, and this is probable. However, only occasional burrows are found opened and abandoned within a day or two after harvest is completed, and few rats remain in the fields. The food supply is limited, cover is gone, and many rodents have been killed outright by machinery. Dead rats and mice can usually be found on the surface in any field with even a moderate population, as soon as the ground is bare. Other carcasses are undoubtedly buried or hauled out with the cane. A substantial segment of the population emigrates from the field to adjacent caneland, gulches, or wasteland; few animals survive and continue to inhabit their old homes.

We made some effort to assess the effects of harvest on our rodent populations. When Field 001 was ready for harvest in August 1961, it harbored moderate and increasing numbers of both *R. exulans* and *M. musculus* (Fig. 5). In anticipation of the harvest, following the final regular mark-and-release sampling of June 20–23, 1961, a trap-out of Grids II and IV was begun on July 18. It extended for 21 days and into the harvest period, until August 7 when harvest operations encroached on this sector of the field. Grids I and III were trapped for the last time on July 25–28 in the routine manner, shortly before harvest began on August 4 in the lower corner of the field adjacent to Kukui Gulch. Harvest progressed over Grids I and III and all the field at that side of the diagonal road crossing it; then operations shifted to the lower side along Kahaupu Gulch and proceeded to cover the rest of the field. Kukui Gulch was last routinely trapped June 14–16; trap-out began there on the night of August 4 as soon as harvest was underway, and continued for 21 days. Each of these several rodent removal operations employed the regular grid or line traps in their usual positions. When equipment no longer disturbed the Grid I and Grid III sites, by August 11, two parallel rows of traps 100 ft apart, each with 32 traps at 50-ft intervals, were set in the bare field. The lines extended from the lower part of Grid III to the upper part of Grid I. An additional 9 traps were placed around a stone pile at the upper corner of Grid I. These 73 traps were operated for 15 days, until August 26 when all trapping was terminated.

There were three objectives in this series of samplings: to test the response of rodents to heavy predation simulated by intensive trap-out, to determine how rapidly the marked segment of the population is decimated by such removal, and to intercept marked and unmarked rodents that survived the harvest. Rodents captured in Kukui Gulch were eliminated like all others, in order to permit access to as many as possible of them without interference by animals already noted there.

Remote from the trapped-out grids, as harvest proceeded in the central part of Field 001, a 0.1-acre circular pen constructed of 18-inch wide strips of sheet metal set on edge, was placed on ground just cleared of cane in order to intercept rodents that might emerge from the soil. Ten traps were placed inside the pen and 10 were placed outside, around the periphery of the pen. In two nights each at three sites, only 1 rodent was caught, a mouse that had emerged from the soil inside the pen. This small sample and the few open burrows in the field demonstrated that few rodents were present in the refugium of the soil when the harvest terminated.

Figure 8 gives results of the several schemes of sampling related to the harvest period. Trap-out of Grids II and IV showed similar patterns, but only data from Grid IV are graphed; all were analyzed. No *R. rattus* were taken. Depletion of marked mice was rapid in the first 7 days, but for the rats it was only moderate in this period, as shown in Table 19. The summary figures of 15.2 percent for mice and 17.8 percent for rats represent marked animals among all those caught. Removal of rodents by trapping may have two prominent effects: to allow remaining animals easier access to traps, and to permit access to the area by peripheral rodents attracted to an area suddenly reduced in population density. Some rodents were still being caught when the sampling ceased, and these were almost all new ones.

TABLE 19

TRAP-OUT RECORD FOR GRID IV, FIELD 001

DAY OF TRAPPING	*M. musculus* CAPTURED	PREVIOUSLY MARKED	PERCENT OF ALL	*R. exulans* CAPTURED	PREVIOUSLY MARKED	PERCENT OF ALL
1–7	139	39	84.8	73	14	53.8
8–14	71	5	10.9	41	8	30.8
15–21	92	2	4.3	32	4	15.4
Summary	302	46	15.2	146	26	17.8

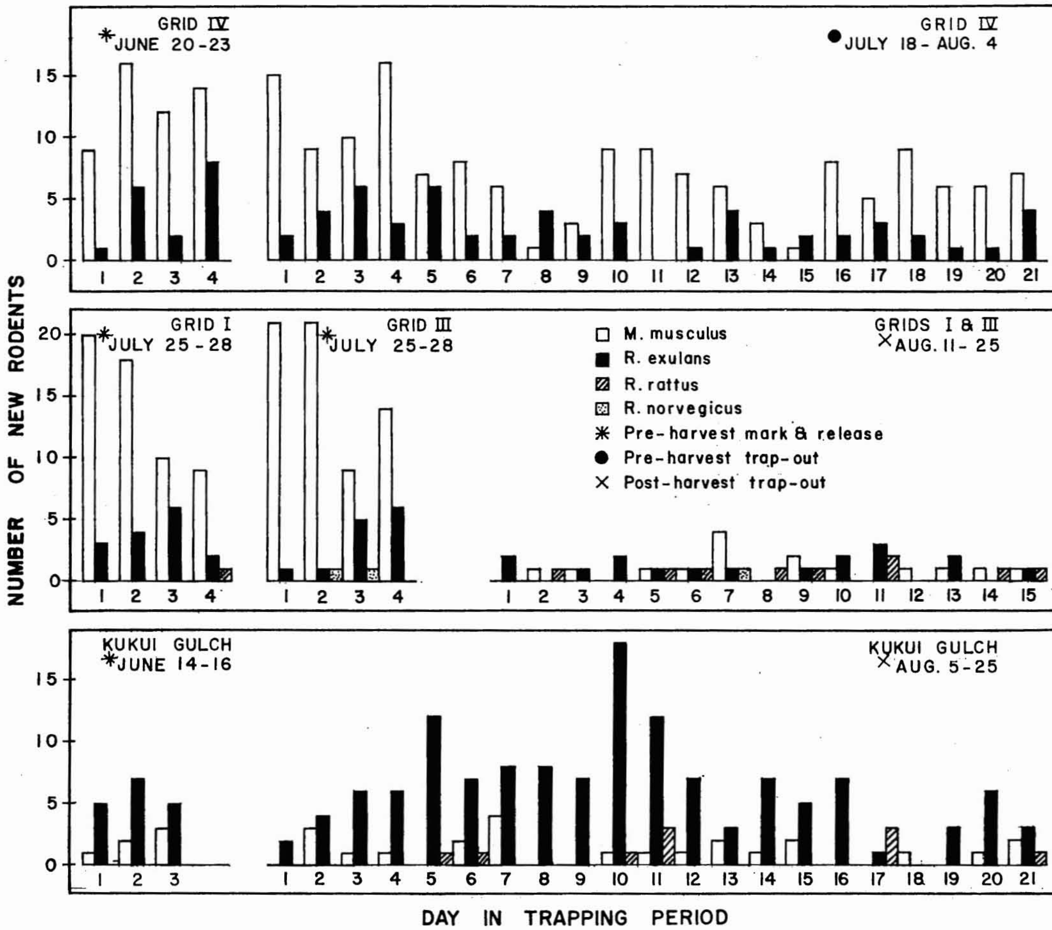

FIG. 8. Summary of preharvest and postharvest rodent trapping, 1959–61 sugar cane crop of Field 001 trapping complex.

In neither species was there evidence that removal of the fellow members of the population or possible influx of strangers modified the movement patterns of the previously marked residents. Av. D showed no tendency to change during 3 weeks of trapping, and was moderate in length for both sexes compared to earlier measures in Field 001 (Tables 1 and 7). The high rate of D = 0 was a good indicator of a probable tendency of the rodents to remain in the vicinity of the trap of previous capture. Low survival in months showed that nearly all the mice had been caught in the previous trapping period, and that nearly all rats were caught in either or both of the two previous periods. These data are presented in the following tabulation. Sexes are combined for *R. exulans* because only 3 of 24 marked residents were males.

	M. musculus		*R. exulans*
	Males	Females	Both sexes
n	21	22	24
av. D	98 ft	77 ft	76 ft
D = 0	23.8%	31.8%	33.3%
Survival	1.2 mo.	1.1 mo.	2.1 mo.

Two marked female mice that entered Grid IV may have been impelled by different forces. One was the last mouse marked in Grid I on July 28, five days earlier, and it had moved 1,980 ft. The other was a resident of Grid III recorded from October 1960 to May 1961, and it moved 1,585 ft to the site of capture in

Grid IV three days after harvest of the Grid III area. A male rat recorded in Grid III on May 18 and 19 also fled to Grid IV, in a similar fashion, having moved 1,375 ft in three days following the harvest of Grid III.

M. musculus was especially common in Grids I and III in the last regular sampling, in July. One *R. rattus* was marked in Grid I, and 2 *R. norvegicus* were marked in Grid III. Although the 73 traps employed in the post-harvest sampling did not cover all of either grid, they did demonstrate presence of a generally sparse population. Of 42 rodents taken, 30 came from the open field and 12 were at the stone piles in the field—15 *M. musculus,* 17 *R. exulans,* 9 *R. rattus,* 1 *R. norvegicus.* Two marked rats were recovered; both were female *R. exulans.* One had been a resident of Grid I between January and May, and was captured on its original range on August 11, five days after the area was cleared. The other had been observed in Grid III in April and May, and it was also on its original range on August 23, 18 days after the cane was burned and raked from the area.

From the stone piles there came 3 *R. exulans,* 8 *R. rattus,* and 1 *R. norvegicus.* This site had been the home of a colony of Norway rats, some of which were recorded in Grid I early in the study, but these appeared to have died out. The 8 *R. rattus* made up nearly 20 percent of all the rodents taken and apparently represented a colony that resided in the stone piles. No marked rodents were caught at the stone piles.

Sexes were about equally divided in the catch.

The small total number of rodents taken shows dramatically the drastic effect that harvest of sugar cane has on field populations, and how some individuals may survive, at least temporarily, in waste areas within the fields, even though these are usually cleared of vegetation by the cane fires. Another aspect is the tenacity that a few animals demonstrate for their old homes, as exemplified by the 2 marked female Polynesian rats taken. This major depletion of the population is especially impressive in view of the fact that no trap-out took place in Grids I and III prior to the harvest.

The Kukui Gulch line was highly productive, the population having been swelled there by animals that fled from the field. A general increase in catch through the 10th day of trap-out in the gulch corresponds to the 9 days of harvest activity in the field. The decline in catch was gradual, suggesting that some stragglers were still coming across the bare field during that time. Rodents caught included gulch residents as well as those from the field. None of 23 *M. musculus* caught was marked, 13 of 132 *R. exulans* were marked, and 9 of these were gulch residents. They showed no unusual characteristics of av. D, % D = 0, or survival time. One of 10 *R. rattus* was marked, but was a gulch resident. The pattern of depletion of the marked gulch rats was similar to that of the field rats subjected to trap-out.

The 4 *R. exulans* not resident in Kukui Gulch came from the following sources: a female marked July 25 in Grid I was caught in the first week of trapping 130 ft away from the site of previous capture in the field; a male also marked in Grid I, in February, was intercepted during the second week, 565 ft from the site of the February capture; a female marked May 18 in Grid III was caught in the second week, 610 ft from its previous capture; a male observed in Grid IV on May 23 and 25 was caught in the third week of gulch trap-out, 1,820 ft from the previous field capture site. Few rats should have been expected from either Grid II or Grid IV after the heavy preharvest trap-out there. That so few marked rats from Grids I and III appeared in the gulch traps suggests relatively heavy mortality from the cane harvest and failure of the gulch line to intercept rats that moved through to the intact Field 33b, just beyond Kukui Gulch.

Captures of *R. rattus* were concentrated in the upper 22 traps of the 54-trap line in Kukui Gulch. Some of these may have been fugitives from the stone piles in the cane field, because 4 came from traps 14 and 16, 450 ft away from one stone pile, and 4 were caught in traps 1 to 7, about 150 ft from another stone pile.

The few *M. musculus* caught in the post-harvest trapping of the Grid I and Grid III sites, and in Kukui Gulch, whether marked or not, is an indication of the fragility of the population in the face of harvest activities. It appears that *M. musculus* is essentially obliterated by the harvest. Grid IV was re-established in October, 2 months after the harvest, and regularly operated each month through February 1962. Of 41 rodents captured in this period, none was a marked animal from the previous crop cycle.

While it seems that many of the *R. exulans* trapped out of Kukui Gulch had emigrated or drifted from Field 001 as the harvest progressed, we have no data to show what their behavior in the gulch might have been had they not been trapped out. Observations in other areas show that when rodents are displaced from a harvested field, they do not register permanent effects on the adjacent gulch population. Field 002, along the far side of Kahaupu Gulch, was harvested on May 17 to 19, 1960, when the gulch-edge rodent population was under close surveillance by means of 2 weeks of operation of the Kahaupu check line each month. The Field 002 population was at a moderate level, but the catch of rats (*R. exulans* and *R. rattus*) did not change appreciably following the harvest. On May 17 only 2 of 8 rats caught were new, on the 18th 3 of 6 were new, and on the 19th and 20th together, 2 of 15 were new. Trapping was resumed during May 24 to 27, when 10 of 18 rats, and 1 mouse, were new animals. This general picture of the catch represents merely normal recruitment to the marked population. Only a small portion of it could possibly be attributed to influx from Field 002.

In another example, Field 101b was harvested during May 12 to 13, 1961. Grid VIII had been trapped out continuously for 30 days, but this had ended 4 weeks before the harvest. Many rodents remained in the field, as was indicated by results of operation of 90 traps spaced at 12-ft intervals along the grassy cliff edge, at the rim of the field, for 8 days, May 12 through 19. The first night of trapping preceded disturbance of the field by harvesting. The catch was 2, 23, 37, 11, 5, 2, 3, and 3—87 in all: 18 *M. musculus,* 58 *R. exulans,* 10 *R. rattus,* and 1 *R. norvegicus*. Two were marked animals from Grid VIII. Thus, the trap line did intercept a significant wave of emigration from the field. The opposite edge of Field 101b, along 101b Gulch, was not trapped out, and it is assumed that a good many rats escaped also from that side of the field. These were permitted to mingle undisturbed with the marked populations of Grids VI and VII which were regularly sampled each month. Operation of Grid VI on May 10 to 13, partly during the harvest, and of Grid VII on May 23 to 26, revealed no influx of new animals, and none marked in the field were included in the catch. Figure 3 shows clearly that seasonal trends in populations were comparable to those in previous years when no harvesting was done. The general conclusion is that displaced rodents do not survive for long, and they do not effectively increase the populations of adjacent gulches, wastelands or cane fields.

Comparative Patterns of Dispersal and Home Range

Graphic patterns of dispersal and lifetime range can be represented by plotting courses of single, exceptionally long moves between grids and lines, or of successive moves of ordinary length, in time. Figure 7 has already illustrated the first of these methods and presents dispersive moves of *M. musculus* from and within Field 001.

In the Spencer Field–Field 33b complex, 8 mice left Grid V in apparently dispersive moves and were caught in adjacent snap-trap lines. These examples were spread over a period of 51 months. For *R. exulans,* when rats were marked only in Grid V, the adjacent Spencer Field and Field 33b snap-trap lines were a cause of heavy mortality among rats that encountered traps in their ordinary daily movements. However, several seem to have made dispersive moves of about the same length as did *M. musculus* during the period from July 1960, when the field was bare, to June 1961 when the cane was well closed over. A similar pattern of movement and dispersal of *R. exulans* was apparent after establishment of Grid X in the adjacent sugar cane. In contrast, *R. rattus* in 54 months at generally low population densities, like *M. musculus,* made few moves between grids and lines, and possibly none of these was a true dispersive move.

In the Field 101b complex where all three rodents were present in moderate to heavy density, *M. musculus* demonstrated rather frequent movement between grids and to the nearby snap-trap line. *R. exulans* made similar moves, but fewer of them. Not many of these could be termed movements of dispersal. *R. rattus* was revealed as a particularly sedentary species, within 101b Gulch. Relatively few moves were recorded for it even between the adjacent Grids VI and VII, and only two were from gulch to cane field.

Although only about half the rodents marked in the study were ever recovered (Table 20), many adequate examples of lifetime ranges were recorded from long-lived individuals frequently recaptured. Figures 9 to 11 demonstrate adjusted range lengths (ARL) and successive moves of representative animals. They were mostly females (only 3 of 15 were males); however, there seem to be no prominent differences in the general pattern of ranges attributable to sex, or for that matter, species. In Grid III of Field 001, *M. musculus* shows a tendency toward elongate ranges (Fig. 9), and this is a typical result of the wide and irregular spacing of the trap rows on the contour ditches. The one female caught 29 times during 14 months presented a remarkable record. She was caught on more than half of the 56 trapping days. She changed range, permanently, by moving on the twelfth capture, after 7 months, to the next irrigation ditch where she remained, as far as our record can tell us, until she disappeared from the population. In Grids VI, VII, and VIII of the Kukuihaele area the tendency of mice to return repeatedly to one or just a few traps was quite obvious, and more strongly marked than in either of the rats, as earlier tables have indicated.

R. exulans moves freely about and tends to cover thoroughly the home range in time (Fig. 10). The male represented left Grid X after 2 months of record and apparently established a new living area in Spencer Field. Grid size seems to be adequate for the demonstration of home ranges in this and all species, even though nearly all ranges include border traps. The small number of ranges that extended into two adjacent grids, however, is good evidence that the ranges, as delineated, present rather accurate pictures of areal use by the several species of rodents, insofar as the mark-and-release system is able to do so.

R. rattus ranges (Fig. 11) cannot be distinguished from those of other rodents in their general conformation. Those selected do average longer than those used for either *M. musculus* or *R. exulans* and suggest that the usual inclination of this species toward fewer captures may be a factor to consider in assessing comparative results of range studies. The male in Grid V of Spencer Field was especially susceptible to capture, and was caught 22 times in just 9 months (36 trap nights). Its ARL, nonetheless, is similar to that of the 2 females each caught 10 times in 9 and 11 months of record.

TABLE 20

PERCENTAGE RECAPTURE OF RODENTS MARKED IN THE SEVERAL TRAP LINES, SEXES COMBINED

	SPECIES OF RODENT							
	Mus musculus		*Rattus exulans*		*Rattus rattus*		*Rattus norvegicus*	
SITE	(n)	%	(n)	%	(n)	%	(n)	%
Field 001	1513	50.0	339	35.4	15	40.0	30	36.7
Kahaupu Gulch	47	21.3	320	47.2	157	40.1	1	0
Kukui Gulch	102	43.1	184	41.8	76	34.2	47	34.0
Field 101b	514	49.4	299	51.5	25	44.0	38	28.9
101b Gulch	395	27.8	304	41.4	315	61.3	19	31.6
Field 33b	192	41.1	169	49.1	35	51.4	0	–
Spencer Field	124	34.7	246	59.3	141	51.1	3	66.7
Summary	2887	44.9	1861	46.1	764	50.9	138	33.3

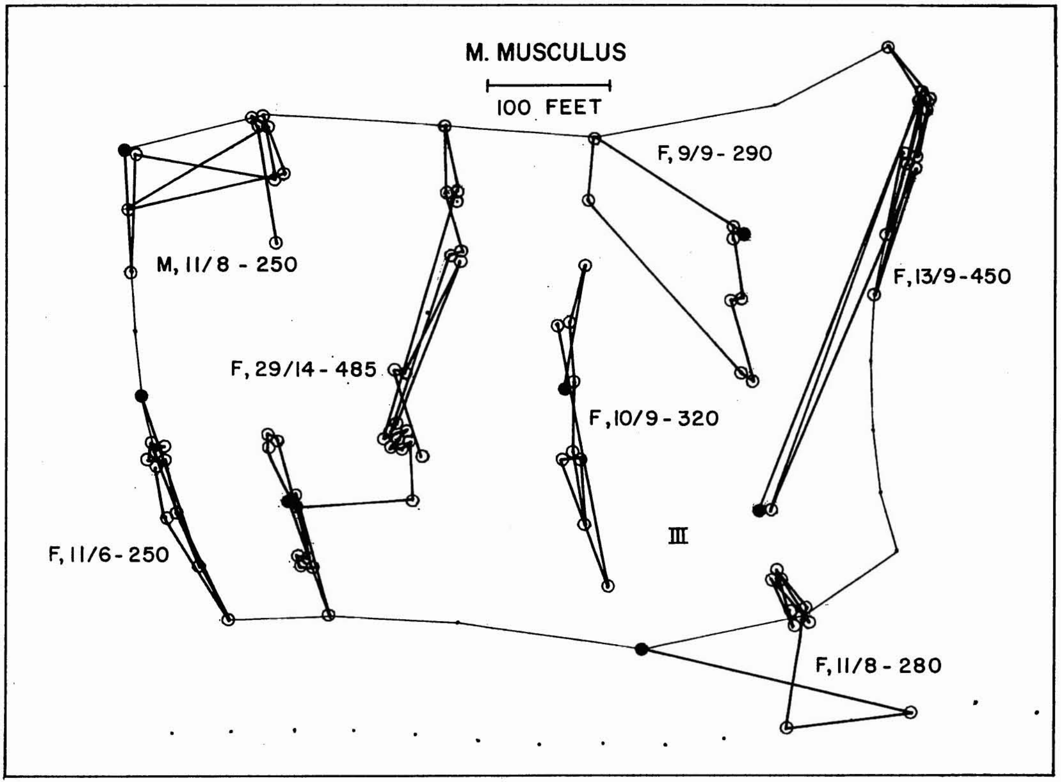

FIG. 9. Selected range maps of individual *Mus musculus* in Grid III, Field 001. Key: Sex, number of captures/months of known survival—adjusted range length in feet. A solid circle identifies the site of first capture; open circles are sites of later captures, connected by lines showing their order of occurrence in time.

DISCUSSION AND CONCLUSIONS

Previous field studies on home range of rodents in Hawaii have been brief (Spencer and Davis, 1950; Kartman and Lonergan, 1955*a*), but have established the general principles that *Rattus exulans, R. rattus,* and *R. norvegicus* are generally sedentary and short lived. The current investigations supply many details lacking from earlier studies, include extensive data on *Mus musculus,* and permit more substantial conclusions than were heretofore possible.

Many parallels exist in the movement patterns of the several rodents studied. In order to compare the three prominent species so that their similarities and differences can be evaluated, summarized data from 12 text tables were graphed (Fig. 12). In the first example (*a*) it is immediately apparent that moves made by males of each species are greater in average length than those of the corresponding females. Average distance between captures (av. D) for rodents repeating capture in less than a month (in the monthly 4-day trapping period) is almost identical in length for *M. musculus, R. exulans,* and *R. rattus.* Rank tests for these data (Table 21) demonstrate that the av. D of 90 ft for male *R. rattus* is significantly longer than that of male *R. exulans* at 82 ft. Other pairs are not statistically different. Rodents recaptured after one or more months (returns) generally make longer moves between captures. Only one of the six pairs of these values for av. D is not statistically different, that for female *R. rattus* at 86 ft and for female *R. exulans* at 91 ft. Thus, with the passage of time, male *R. rattus* have a longer av. D than male *R. exulans* and male *M. musculus;* and for *R. exulans* it is greater than for *M. musculus.* Female *R. rattus* and female *R. exulans* each have a longer av. D than do female *M. musculus.* In these compari-

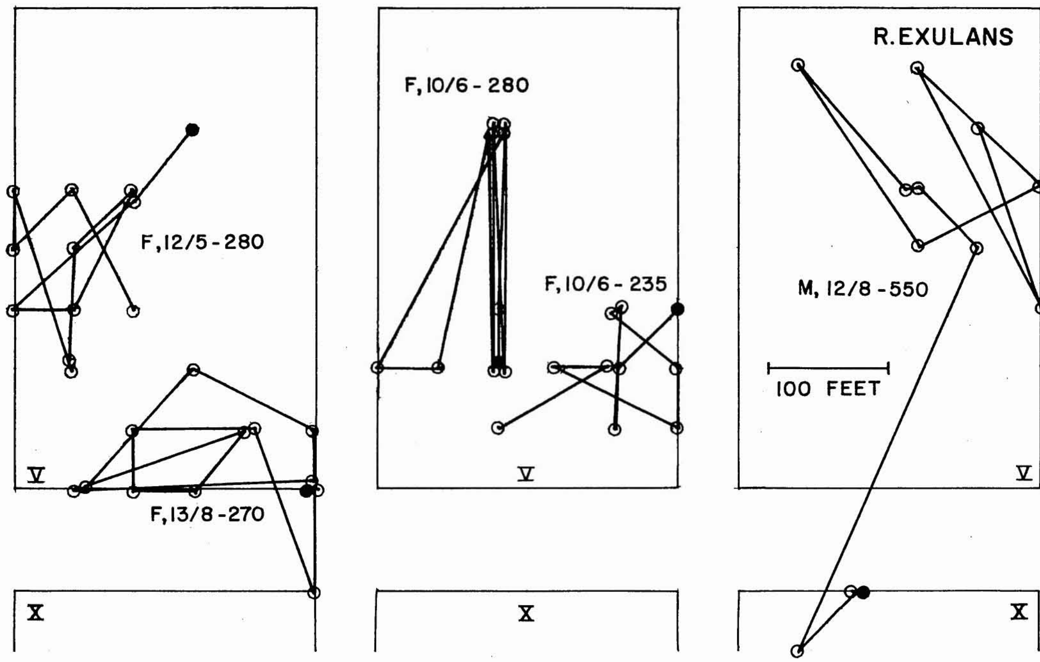

FIG. 10. Selected range maps of individual *Rattus exulans* in Grid V of Spencer Field and Grid X of Field 101b. Key as for Figure 9.

sons the general trend is established that in everyday activity all species make moves of generally similar length; but in correlation with body size, the larger species range for greater distances than do the smaller species when successive captures occur at monthly or longer intervals. Also, the tendency for greater mobility is stronger in males than in females.

Adjusted range length (Fig. 12*b*) is an expression of the extent of use of the habitat during the lifetime of a rodent. It follows some trends by species and sex that are identified with

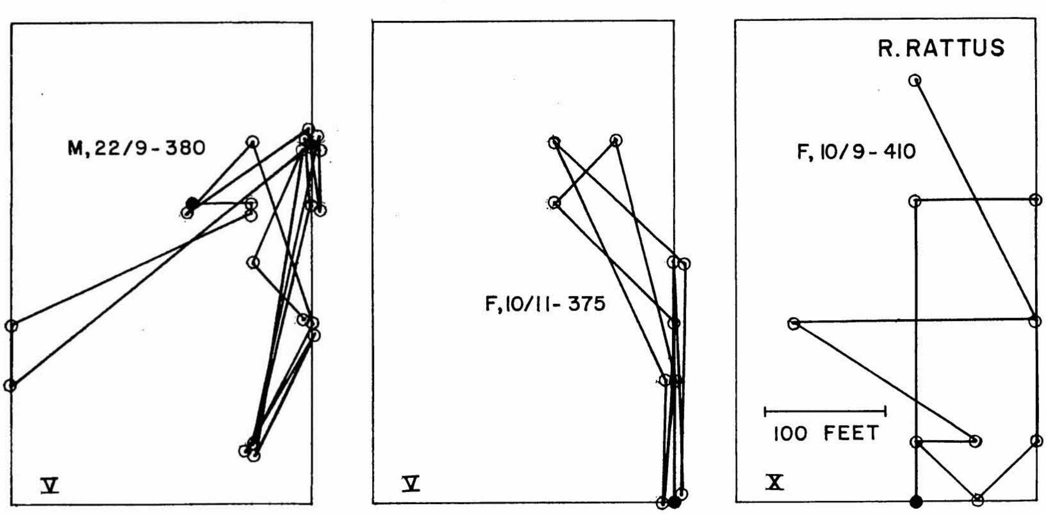

FIG. 11. Selected range maps of individual *Rattus rattus* in Grid V of Spencer Field and Grid X of Field 33b. Key as for Figure 9.

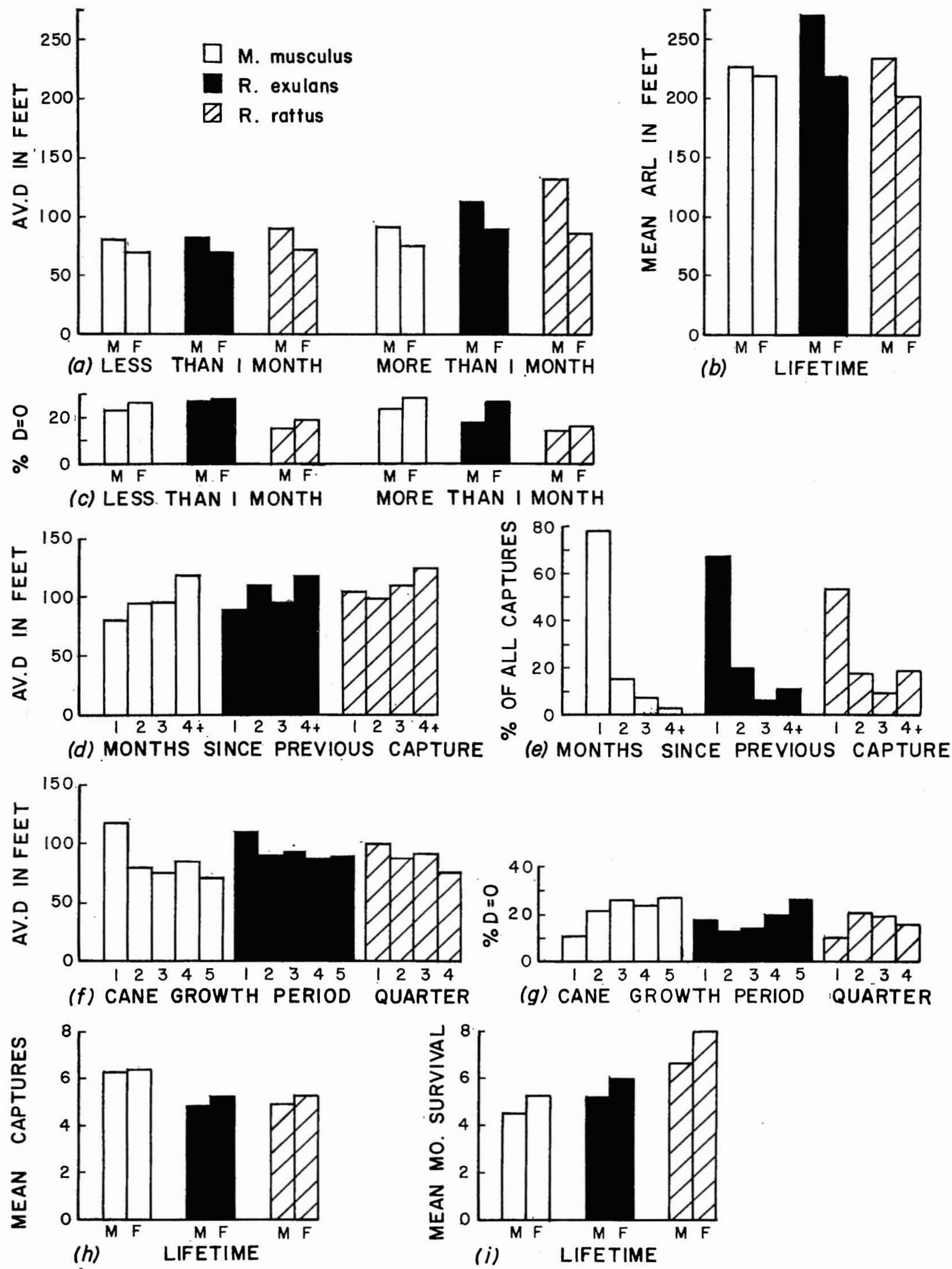

FIG. 12. Summary of mean values in various aspects of movement patterns of rodents, comparing the three prominent species. Graphs read in sequence from (*a*) through (*i*). Data were derived as follows: (*a*) and (*c*) from Tables 1, 7, 13; (*b*), (*h*), and (*i*) from Tables 6, 11, 16; (*d*) and (*e*) from Tables 2, 8, 14; (*f*) and (*g*) from Tables 3, 9, 15.

TABLE 21

PROBABILITIES OF DIFFERENCES IN AVERAGE DISTANCE BETWEEN CAPTURES (av. D) FROM RANK TESTS AMONG THREE RODENTS, BY LIKE SEX AND BY TIME INTERVAL BETWEEN INDIVIDUAL CAPTURES
(R, Repeat within the 4-day trapping period; R1, return after one or more months)

			Rattus rattus											
			R						R1					
			M			F			M			F		
			av. D	(n)	P	av. D	(n)	P	av. D	(n)	P	av. D	(n)	P
Mus musculus														
	R	M	90	(178)	.125									
			81	(776)										
		F				73	(194)	.386						
						69	(535)							
	R1	M							132	(250)	.000**			
									91	(739)				
		F										86	(269)	.002**
												75	(613)	
Rattus exulans														
	R	M	90	(178)	.038*									
			82	(413)										
		F				73	(194)	.184						
						70	(406)							
	R1	M							132	(250)	.009**			
									113	(328)				
		F										86	(269)	.378
												91	(493)	

			Rattus exulans											
			R						R1					
			M			F			M			F		
			av. D	(n)	P	av. D	(n)	P	av. D	(n)	P	av. D	(n)	P
Mus musculus														
	R	M	82	(413)	.164									
			81	(776)										
		F				70	(406)	.261						
						69	(535)							
	R1	M							113	(328)	.015*			
									91	(739)				
		F										91	(493)	.003**
												75	(613)	

* Significant (P < .05).
** Highly significant (P < .01).

the study of av. D, and is generally 2 to 3 times the length of av. D. Males tend to range farther than females, but the increase of range with body size is not apparent among the various species. Such effects actually present may be masked by a more frequent change of home site by the small (ca. 12 g) *M. musculus,* the "normal" behavior of the intermediate-weight (ca. 50 g) *R. exulans,* and the greater use of the three-dimentional habitat to include trees, by the large (ca. 125 g) *R. rattus.* However, no specific data are available to demonstrate this reasoning. In the absence of such definitive information the conclusion must be drawn that adjusted range lengths are similar in all species. The obviously long range of male *R. exulans,* at 272 ft, is significantly greater than that for females of the same species, at 219 ft, but none of the eight other comparisons made, by like sex between species and by opposite sex within species (Table 22), demonstrates statistical differences.

The tendency to return to the trap of previous capture (Fig. 12 *c*), in which case no distance of movement is measurable (D = 0), is about the same overall for *M. musculus* and *R. exulans,* but appreciably less in *R. rattus.* This trait is expressed less strongly in time by *R. exulans* and *R. rattus,* but not by *M. musculus,* in which it is about the same among animals repeating in the 4-day trapping period and those returning after a month or longer. In the measure D = 0 there is an obvious shift to larger percentage figures for females than for males, in all classes. This is inversely correlated with lengths of av. D shown in Figure 12 *a,* as would be expected, because the farther a rodent ventures from home the more traps it will encounter, as long as it remains within the local system of traps.

Av. D by the number of months elapsed since previous capture shows a general upward trend with time (Fig. 12 *d*), although some irregularities are apparent. For each species the largest difference occurs between the 3-month interval and all succeeding months. This suggests that as long as a rodent is alive there is some probability that it will move for a greater distance than on any previous move. An explanation seems to lie in changes of residence that occur in time, and in unusual changes in the environment that are only occasional, and which may force movement to habitat not usually occupied. In Figure 12 *e* the comparative lengths of life are reflected, as is the behavioral trait of frequency of recapture within specified time brackets. *M. musculus* has the highest rate of return within 1 month, *R. exulans* is second, and *R. rattus* is third, in the reverse order of body size and of longevity.

In the arbitrarily selected 4-month growth periods of sugar cane (Fig. 12*f*), as the crop develops and matures there is surprisingly little response by either *M. musculus* or *R. exulans* to the vast changes in character of the habitat. However, av. D is obviously longer in both species when food and cover, in the form of cane and weeds, are sparse and the rodents few in number. Importantly, though fluctuations of large amplitude occur in population densities after the cane closes over, the rodents do not change appreciably their habits of distances moved. *R. rattus,* whose data came from stable gulch habitats (and are arrayed by quarters of the year), appears to have a shorter av. D in the fourth quarter of the year than in others, and this may be a true seasonal response.

The frequency of D = 0 is generally less early in the cane crop than later, for both *M. musculus* and *R. exulans* (Fig. 12*g*), which suggests, again, that increase of associated weeds rather than greater densities of population is effective in influencing how far the rodents will move in relation to the trap of previous capture. In the gulch-inhabiting *R. rattus* the tendency to enter different traps gains increasingly from the second quarter around through the first, for the percentage of returns to the trap of previous capture steadily decreases on this same schedule.

Frequency of capture of the individual rodent (Fig. 12 *h*) is outstandingly higher in *M. musculus* than in either *R. exulans* or *R. rattus,* in which species the data are almost identical. Survival in months (or if preferred, residence or longevity) in the graph labeled (*i*), on the other hand, gains steadily with increase of body size in the several species. However, by actual proportion to weight, the tiny *M. musculus* lives longer than either of the relatively large rats. There is an apparent correlation between greater longevity in female rodents and their

TABLE 22

PROBABILITIES OF DIFFERENCES IN ADJUSTED RANGE LENGTHS (ARL) FROM RANK TESTS AMONG THREE RODENTS, BY LIKE SEX BETWEEN SPECIES, AND BY OPPOSITE SEX WITHIN SPECIES

	Rattus rattus						*Rattus exulans*						*Mus musculus*		
	M			F			M			F			F		
	ARL	(n)	P	ARL	(n)	P	ARL	(n)	P	ARL	(n)	P	ARL	(n)	P
Mus musculus															
M	235 228	(52) (147)	.456				272 228	(91) (147)	.081				219 228	(104) (147)	.097
F				203 219	(73) (104)	.152				219 219	(101) (104)	.492			
Rattus exulans															
M	235 272	(52) (91)	.174							219 272	(101) (91)	.022*			
F				203 219	(73) (101)	.201									
Rattus rattus															
F	235 203	(52) (73)	.067												

* Significant ($P < .05$).

greater frequency of capture. Males are relatively short lived and register fewer captures. It seems probable, however, that the mean number of captures is less variable than the mean months of survival, suggesting that males are more aggressive than females in entering traps. In general, sample sizes of males are considerably larger than those of females, both in numbers of new animals marked and in total captures.

All species are characteristically sedentary and often the entire life span is spent within an area less than 400 ft across. *R. exulans* is highly adapted to all habitats and its populations are more evenly continuous across the study region than are others. *R. rattus* is best suited to gulches and wooded habitats, hence its populations tend to be continuous from sea level to the higher forests, but discontinuous in the cane fields between gulches. It is the least mobile with regard to dispersal. *M. musculus* may disperse quite often for distances up to 0.5 mile, especially from centers of high population density. *R. exulans* tends to make relatively long moves (up to 1,000 ft) from its usual home range, and occasionally to return to it. *R. norvegicus* continued to be unimportant from 1961 onward and virtually disappeared from all field habitats.

Jackson and Strecker (1962, pp. 117–123) have reviewed numerous studies of *R. exulans* and *R. rattus,* and have presented new data from the Caroline Islands. It is fair to conclude that their statement (p. 121), "The considerable variance in data from different areas reflects environmental differences and probably differences in trapping methods as well," is a sound one. Thus, there seems no object in attempting close comparisons between the current results from Hawaii and those from other studies. It should suffice to declare them similar. A major objective of our work has been to study the four field rodents of Hawaii together in the local setting and to learn what their comparative similarities and differences are with regard to movement patterns. Other studies of *M. musculus,* for example, those of Lidicker (1966, pp. 30–35) and of Quadagno (1968) also support the conclusion of Jackson and Strecker. Crowcroft (1955) studied confined populations of *M. musculus* and revealed a strong influence of social interaction in the shaping of location, boundaries, and size of home range. I am aware of no true field studies of *R. norvegicus,* but Davis et al. (1948) and Davis (1953) made thorough investigations of populations among farm buildings and in an urban slum. Here, relatively stable conditions of food and shelter, and social pressures enforced a notably restricted pattern of movement suggestive of that found in confined mice. Yet it was similar in the overall pattern to that in sugar cane fields of Hawaii. It is evident, then, that social factors are among the prominent elements of the environment. That they act in sparse populations as well as in dense ones is probable, but at different levels of intensity.

Tomich and Haas (1966) and Tomich (1968*b*) have reviewed some of the implications for rodent control extracted from this study. It is apparent that social factors not treated in this work should also receive a share of attention as an important aspect of rodent ecology. Calhoun (1962) examined in detail the matter of theory for approaching rodent control from the point of view of behavior of the rodents. He made the suggestion, based on interdependency of social interaction and movement in rodent populations, that control measures in agricultural regions might well be applied almost exclusively to the fringes of croplands rather than to the fields themselves.

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